

1
M183
40.15
Bot

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XV

1959-1960

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, *Chairman*

EDCAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California

HERBERT F. COPELAND, Sacramento College, Sacramento, California

JOHN F. DAVIDSON, University of Nebraska, Lincoln

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts

MILDRED E. MATHIAS, University of California, Los Angeles

MARION OWNBEY, State College of Washington, Pullman

IRA L. WIGGINS, Stanford University, Stanford, California

SECRETARY, EDITORIAL BOARD

ANNETTA M. CARTER, Department of Botany, University of California, Berkeley

BUSINESS MANAGER AND TREASURER

WINSLOW R. BRIGGS, Department of Biology, Stanford University,
Stanford, California (1959)

JOHN H. THOMAS, Dudley Herbarium,
Stanford University, Stanford, California (1960)

Published quarterly by the
California Botanical Society, Inc.

2016 Life Sciences Building, University of California, Berkeley

Printed by Gillick Press, Berkeley, California



UNIVERSITY OF CALIFORNIA
LIBRARY
PCT 2 - 587



R. C. Frampton Photo, Claremont

TO PHILIP ALEXANDER MUNZ, teacher of botany, student of the Onagraceae, author of two California floras and, until his recent retirement, Director of the Rancho Santa Ana Botanic Garden, the California Botanical Society dedicates this, its fifteenth volume of *Madroño*.

During his many years of teaching, Philip Munz has held professorships at Pomona College, Cornell University, and presently at Claremont Graduate School. In addition to the two floristic works, his scientific writings have included monographic studies of both North and South American plant groups. On quite another level, however, many regard his greatest achievement to be what he has made of the Rancho Santa Ana Botanic Garden of the native plants of California. Here, during the past fifteen years, all his talents and accomplishments have been turned to the purpose of creating a model botanical institution, one which has become an increasingly renowned center for research upon all phases of the California flora. Well-founded in his judgments, forward-looking yet moderately conservative in his administration, encouraging to achievement in other fields than his own, wise in his choice of personnel, his rare qualities of leadership have brought his institution to a point of high repute in the botanical world. Beloved by his colleagues and genuinely young-in-heart, he is looked upon by his staff as the benevolent head of his "family."

v.15
1959-60
Botany

CONTENTS

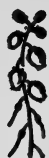
PAGE

Frontispiece: Philip Alexander Munz	
Survival of transplanted Cupressus in the pygmy forests of Mendocino County, California— <i>Calvin McMillan</i>	1
An interspecific cross in Cucurbita (<i>C. lundelliana</i> × <i>C. moschata</i> Duch.)— <i>Thomas W. Whitaker</i>	4
The reproductive structures of Schinus Molle (Anacardiaceae)— <i>Herbert F. Copeland</i>	14
Development of the megagametophyte in Liquidambar styraciflua L.— <i>Franklin F. Flint</i>	25
Reviews	29, 62, 94, 158, 192, 221, 249
Notes and News	32, 63, 96, 128, 160, 192, 222
Red algal parasites occurring on members of the Gelidiales— <i>Kung-Chu Fan</i> and <i>George F. Papenfuss</i>	33
Xerophyllum tenax, squawgrass, its geographic distribution and its behaviour on Mount Rainier, Washington— <i>Sue Merrick Maule</i>	39
Documented chromosome numbers of plants	49, 219
Typification of Prosopis odorata Torr. and Frem. (Leguminosae)— <i>Lyman Benson</i>	53
Two new species of Helianthus from New Mexico— <i>R. C. Jackson</i>	54
Chromosome counts in the section Simiolus of the genus Mimulus (Scrophulariaceae). III— <i>Barid B. Mukherjee</i> and <i>R. K. Vickery, Jr.</i>	57
Factors affecting the distribution of Ponderosa and Jeffrey pines in California— <i>John R. Haller</i>	65
Vivipary in Cordyline australis Hook.— <i>Howard J. Arnott</i>	71
Studies on secotiaceous fungi VI. Setchelliogaster Pouzar— <i>Rolf Singer</i> and <i>Alexander H. Smith</i>	73
Ceanothus seeds and seedlings on burns— <i>Clarence R. Quick</i>	79
Chromosome numbers of California plants, with notes on some cases of cytological interest— <i>Richard Snow</i>	81
Chromosome counts in the genus Gayophytum— <i>David G. Dixon</i>	90
The grass genera Orcuttia and Neostapfia: a study in habitat and morphological specialization— <i>Beecher Crampton</i>	97
The taxonomic relationship between Picea glauca (Moench) Voss and P. engelmannii Parry— <i>T. M. C. Taylor</i>	111
Field studies of natural hybridization in the Oregon species of Iris L. subsection Californicae Diels— <i>Quentin D. Clarkson</i>	115
Variation patterns in four clones of Mertensia ciliata— <i>Jeanette S. Pelton</i>	123
New combinations in Aster— <i>Roxana S. Ferris</i>	128
The distribution of dwarf mistletoes, Arceuthobium, in California— <i>Job Kuijt</i>	129
Nuclear cytology of the California mouse-tails (Myosurus)— <i>Donald E. Stone</i>	139
Variation in section Trigonophyllae of Nicotiana— <i>Philip V. Wells</i>	148

Studies on secotiaceous fungi VII. Secotium and Neosecotium— <i>Rolf Singer and Alexander H. Smith</i>	152
The reproductive structures of <i>Fraxinus velutina</i> (Oleaceae)— <i>Herbert F. Copeland</i>	161
A new <i>Silene</i> from northwestern California— <i>A. R. Kruckeberg</i>	172
Freed Hoffman— <i>John L. Morrison</i>	178
Cleared <i>Cardiocarpon late-alatum</i> Lesq., Cordaitean seeds from Michigan— <i>J. F. Davidson</i>	180
The basic chromosome number of the genus <i>Neptunia</i> (Leguminosae- Mimosoideae)— <i>B. L. Turner and O. S. Fearing</i>	184
Hybridization and instability of <i>Yucca</i> — <i>John Milton Webber</i>	187
<i>Sanicula deserticola</i> , an endemic of Baja California— <i>Peter H. Raven and Mildred E. Mathias</i>	193
A new species of <i>Valeriana</i> from Brazil— <i>Frederick G. Meyer</i>	197
Studies in western violets, IX. Miscellaneous species in the sections <i>Nomimium</i> and <i>Chamaemelanium</i> — <i>Milo S. Baker</i>	199
Chromosome numbers in <i>Silene</i> (Caryophyllaceae). II.— <i>A. R. Kruckeberg</i>	205
A new species of <i>Zinnia</i> from Mexico— <i>A. M. Torres</i>	215
A comment on cold susceptibility of <i>Ponderosa</i> and <i>Jeffrey</i> pines— <i>Willis W. Wagoner</i>	217
Distributional notes on plants of the Warm Springs area, Oregon— <i>Robert Ornduff and David H. French</i>	225
G. Thomas Robbins (1916–1960)— <i>Rimo Bacigalupi</i>	231
Studies in the perennial gentians: <i>G. newberryi</i> and <i>G. tiogana</i> — <i>Charles T. Mason, Jr.</i>	233
Chromosome counts in the section <i>Simiolus</i> of the genus <i>Mimulus</i> (Scrophulariaceae). IV.— <i>Barid B. Mukherjee and Robert K. Vickery, Jr.</i>	239
Flowering responses in <i>Phacelia sericea</i> and <i>P. idahoensis</i> — <i>George W. Gillett</i>	245
Index to Volume XV.....	253

ERRATA

- Page 25, line 12: *for* Juliano, J. M., *read* Juliano, J. B.
Page 48, line 34: *for* 1951 *read* 1925.
Page 51, line 11: *for* Connty *read* County.
Page 71, line 15: *for* 1928 *read* 1950.
Page 138, line 7: *for* *existes* *read* *exists*.
Page 138, line 16, *for* 1914 *read* 1913.
Page 139, line 13: *for* 1914 *read* 1913.
Page 188, line 1: *for* *hybirds* *read* *hybrids*.
Page 199, line 20: *for* *terrano* *read* *terraneo*.
Page 199, line 21: *for* *subterreno* *read* *subterraneo*.
Page 199, line 26: *for* *marginis* *read* *marginibus*.
Page 213, line 52: *for* *australe* *read* *australis*.
Page 220, line 30: *for* *phyllocephallus* *read* *phyllocephalus*.



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 1

JANUARY, 1959

Contents

	PAGE
SURVIVAL OF TRANSPLANTED CUPRESSUS IN THE PYGMY FORESTS OF MENDOCINO COUNTY, CALIFORNIA, <i>Calvin McMillan</i>	1
AN INTERSPECIFIC CROSS IN CUCURBITA (<i>C. LUNDELLIANA</i> × <i>C. MOSCHATA</i> DUCH.), <i>Thomas W. Whitaker</i>	4
THE REPRODUCTIVE STRUCTURES OF <i>SCHINUS MOLLE</i> (ANACARDIACEAE), <i>Herbert F. Copeland</i>	14
DEVELOPMENT OF THE MEGAGAMETOPHYTE IN <i>LIQUIDAMBAR STYRACIFLUA</i> L., <i>Franklin F. Flint</i>	25
REVIEWS: John Thomas Howell, Peter H. Raven, and Peter Rubtzoff, <i>A Flora of San Francisco, California</i> (John H. Thomas); Gerd Krüssmann, <i>Die Nadelgehölze</i> (Baki Kasapligil)	29
NOTES AND NEWS	32

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—WINSLOW R. BRIGGS.

Department of Biology, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: James R. Sweeney, San Francisco State College, San Francisco, California. First Vice-president: Baki Kasapligil, Mills College, Oakland, California. Second Vice-president: Henry J. Thompson, Department of Botany, University of California, Los Angeles, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: Winslow R. Briggs, Department of Biology, Stanford University, Stanford, California.

SURVIVAL OF TRANSPLANTED CUPRESSUS IN THE PYGMY FORESTS OF MENDOCINO COUNTY, CALIFORNIA

CALVIN McMILLAN

In a recent study of the edaphic restriction of *Cupressus* and *Pinus* in central California (McMillan, 1956), certain species from highly acid soils and from serpentine soils were investigated. Soil tolerance studies conducted both under greenhouse conditions and in large outdoor bins were used in this inquiry.

One phase of the investigation not previously reported involved the transplanting of seedling trees to the habitat of the pygmy forest in Mendocino County. At the time of the transplanting no extended analysis of seedling survival was anticipated. Since it has been possible to continue the observations, however, this report will evaluate the survival over a period of seven years.

The pygmy forests have been described adequately elsewhere (McMillan, 1956), but certain features of the transplant site on the coastal plateau between the Little and Albion rivers are pertinent. The transplant area, approximately one mile southwest of the Mendocino County Airport, was on the property of Miss Jean MacGregor Boyd. It had been subjected to previous burnings and was covered by a low growth of trees and shrubs. The site was included within the narrow restriction of both *Cupressus pygmaea* (Lemm.) Sarg. and *Pinus bolanderi* Parl., and both species were represented by numerous individuals varying in height from 25–100 cm. *Vaccinium ovatum* Pursh, *Rhododendron californicum* Hook., and *Gaultheria shallon* Pursh were common shrubs of the area. *Arctostaphylos nummularia* Gray, a species which does not crown-sprout following burning, was represented by a few small shrubs. In adjacent areas with no record of recent burning, *Arctostaphylos* was common with *Pinus muricata* Don. The dense *Sequoia-Pseudotsuga* forest, common on the margins of the plateau, was adjacent to the transplant site. The soil in the transplant garden is a ground-water podsol with a pH of 3.8–4.0. This ashy-colored soil, which is common throughout the areas of the pygmy forest, is usually less than a foot in depth and is one of the most acid soils in California.

Seedlings of the various strains of *Cupressus*, including those of *C. pygmaea*, *C. goveniana* Gord., *C. abramsiana* C. B. Wolf, and *C. sargentii* Jeps., were transplanted from the greenhouse at Berkeley to the pygmy forest in November, 1950. Six of each strain were planted in each of two series. One group was protected from browsing animals by a large wire screen cage, while the second series remained unprotected. The unprotected seedlings were severely damaged and could not be used in the study. The cage protected the other seedlings throughout the investiga-

tion. Measurements were recorded at intervals beginning at the date of planting and continuing until August, 1957.

In April, 1952, individuals of the two strains of *C. pygmaea* from Mendocino County (one from the pygmy forest area, the other from Anchor Bay) were dark green and vigorous. Individuals of the two strains of *C. goveniana* from Monterey County (one from Huckleberry Hill and the other from behind Point Lobos) and the one strain of *C. abramsiana* (from Bonny Doone in the Santa Cruz Mountains) were lighter green and lacked vigor. The average growth increment since transplanting showed clearly that the *C. pygmaea* strains were the most vigorous even though the actual increase in height for all strains was slight. Seedlings of *C. sargentii* (from a serpentine area on Mt. Tamalpais in Marin County) were barely surviving in 1952.

Over the same two-year period, seedlings were grown at Berkeley in large outdoor bins containing soil from the habitat of the pygmy forests. These bins were used until 1952 and at that time the responses of the strains reversed the trend indicated in the transplant garden. The vigor and height of the two strains of *C. pygmaea* was less than that of either *C. goveniana* or *C. abramsiana*. In contrast, seedlings of all strains grew well at Berkeley in bins containing an agricultural type of soil. The *C. pygmaea* strain from the pygmy forests was extremely vigorous on the agricultural soil and had an average height of 82 cm. after the 2-year growth period (McMillan, 1956). This contrasts sharply with a 3.3 cm. average height increase of the same strain when transplanted to the pygmy forest habitat.

In August, 1954, the transplant garden was observed after an interval of two years. The growth differential which had been apparent in 1952 was intensified. The trees of *C. pygmaea* were much more vigorous than those of either *C. goveniana* or *C. abramsiana*. Of the surviving strains, only that from Pt. Lobos failed to show an increase in height over 1952 measurements. All of the individuals of *C. sargentii*, the only strain from serpentine soils, had died during the interval.

Observations at the transplant garden in August, 1957, indicated considerable development of both strains of *C. pygmaea*. Somewhat greater vigor characterized the individuals of the pygmy forest strain. Average growth since transplanting was 11.8 cm. The average height increase for the Anchor Bay strain was 9.3 cm. These strains of *C. pygmaea* produced pollen-bearing cones and only the pygmy forest strain had produced a mature seed-bearing cone.

Much less growth and a reduction in the number of surviving trees were noted in *C. goveniana* and *C. abramsiana*. None of the trees of the Point Lobos strain of *C. goveniana* survived. The four surviving trees of the Huckleberry Hill strain had grown very slightly and none was vigorous. Only two of the *C. abramsiana* individuals were surviving and these showed only a trace of height increase.

The growth pattern of dwarfed trees of *C. pygmaea* results from a

unique tolerance for the highly acid soils of the pygmy forest area. At the transplant site, small, cone-bearing trees, varying between 25 and 50 cm. in height, had 21 growth rings when measured in 1952. These trees were less than 70 cm. in 1957. Other trees, in pygmy forest areas adjacent to the transplant site, had over 100 growth rings, a 6–10 cm. diameter and a height of less than 2 m. A few larger trees (30–50 m.), such as those measured by Mathews (1929), indicate the type of growth which can be achieved under conditions which support mostly *Sequoia* and *Pseudotsuga*.

Although the survival pattern in *Cupressus* indicates that the strain from the pygmy forests is the best fitted for growth on the highly acid soils in Mendocino County, it must not be inferred that the other strains are incapable of the growth pattern producing a pygmy forest. For example, at Huckleberry Hill, trees of *C. goveniana* closely resemble *C. pygmaea*. Although occasional tall trees of *C. goveniana* occur with *Pinus radiata* Don, the majority of the trees with *P. muricata* give an appearance of a pygmy forest. The inability of the Huckleberry Hill strain to grow well at the transplant garden in Mendocino County is particularly difficult to explain on an edaphic basis because of the marked similarity of the soils of the two areas. Climatic conditions of Mendocino County suggest a more likely explanation. However, trees of *C. macrocarpa*, a species also restricted to the Monterey Peninsula in its natural distribution, are thriving and reproducing along the Mendocino County coast. Unless the climatic tolerances of *C. macrocarpa* and *C. goveniana* differ markedly, the explanation would lie possibly in the action of the highly acid soils in conjunction with the cooler temperatures of the more northern location. Extended periods of freezing temperatures and of dry summer conditions occurred between 1954 and 1957. This may have provided the critical point for reduced survival among all of the strains from the more southerly localities and, in particular, produced conditions beyond the tolerance of the Point Lobos strain of *C. goveniana*. The loss of seedlings of *C. sargentii* early in the study may indicate a low survival potential on highly acid soils by strains from serpentine soils.¹

Studies of the nature of restriction of *Cupressus pygmaea* indicate that the species is not confined to the pygmy forests because of an inability to grow elsewhere. The restriction results, in part, from the tolerances of *C. pygmaea* for conditions resulting in a dwarfed form and, in part, from the lack of tolerance by taller forms, such as *Sequoia* and *Pseudotsuga*, for growth on the shallow, highly acid soils. Furthermore, these survival studies indicate that *C. pygmaea* possesses a tolerance not shared by the strains of other species of *Cupressus* for conditions of the pygmy forest habitat.

¹ Preliminary studies indicate that day length factors were not critical in the differential survival of the Huckleberry Hill and Mendocino seedlings. In greenhouse studies, seedlings of the Monterey strain as well as seedlings of both Mendocino strains responded similarly to a range of light periods: 8-hour, 12-hour, and 16-hour.

Selective influences on the coastal plateau of Mendocino County have sorted out a combination of species with unique qualities for survival in one of the most extreme soil situations in California. The pygmy forests which have resulted from this selective action include much of the natural distribution of both *Cupressus pygmaea* and *Pinus bolanderi*. The gigantic *Sequoia-Pseudotsuga* forests which grow in adjacent portions of the coastal plateau present an amazing contrast in vegetational selection.

Department of Botany
University of Texas
Austin, Texas

LITERATURE CITED

- MATHEWS, W. C. 1929. Measurements of *Cupressus pygmaea* Sarg. on the Mendocino "pine barrens" or "white plains." *Madroño* 1:216-218.
McMILLAN, C. 1956. The edaphic restriction of *Cupressus* and *Pinus* in the Coast Ranges of central California. *Ecological Monographs* 26:177-212.

AN INTERSPECIFIC CROSS IN CUCURBITA (*C. LUNDELLIANA* BAILEY \times *C. MOSCHATA* DUCH.)

THOMAS W. WHITAKER¹

As one aspect of a comprehensive study of the origin and relationship of the cultivated species of *Cucurbita*, *C. lundelliana* Bailey, a non-cultivated species, was crossed with *C. moschata* Duch., one of the five cultivated species of the genus. In *Cucurbita* successful crosses between truly wild species and domesticated ones have not been hitherto reported. Essentially the cross *C. lundelliana* \times *C. moschata* combines two genotypes, the one (*C. lundelliana*) a wild species and the other (*C. moschata*) with a long history of cultivation. The hybridization experiments reported here were made with the idea that the compatability relations might indicate directions in which to search for the common ancestor of the cultivated group, and perhaps suggest in a general way the area where the cultivated forms were domesticated (Whitaker, 1956). Furthermore, it was thought that the results would contribute to an understanding of the heritability of characters such as large fruit, large seed, soft rind, etc., which have value under cultivation. The results reported here provide partial answers to some of these questions.

MATERIALS AND METHODS

Cucurbita lundelliana, the Peten gourd, is endemic in Central America. It has been collected in Guatemala, British Honduras, and southern Mexico (Yucatan). The plants are strong, vigorous annuals, with fine,

¹ This study was aided by a grant from the American Academy of Arts and Sciences. I am much indebted to Professor Edgar Anderson, Curator of Useful Plants, Missouri Botanical Garden, for helpful suggestions and advice. My thanks are due to G. A. Sanderson, Agricultural Aid, for the photographs and to M. A. McClure, Technician, for preparing figure 4.

wiry stems and deeply lobed leaves having a greyish-green cast (fig. 1B). The flowers of both sexes are large, showy and upright (fig. 1E). The fruits are almost round, dark green, often striped, and have hard rinds, or shells (fig. 2A). The flesh is greenish white and the placenta is solid. The seeds are comparatively small and numerous and have characteristic broad, wavy margins.

Cucurbita moschata cv. Long Genoa Queen is an old and little-known cultivar quite typical of the species. The modern cultivar Butternut of *C. moschata* probably originated as a selection from Long Genoa Queen. The plants have good vigor, large, ovoid leaves, slightly triangular lobed (fig. 1A); long fruits (19 to 36 inches), with an enlarged terminal portion that contains the seeds (fig. 2B). The flesh is dark-orange, moist and slightly stringy.

Both *C. lundelliana* and *C. moschata* have 20 pairs of chromosomes. Unfortunately, it has not been possible to study cytologically the progenies of the cross between them.

Matings of *C. lundelliana* and *C. moschata* cv. Long Genoa Queen produced fruits with numerous fertile seeds. The F_1 proved to be self-fertile and cross-fertile with each parent. In the summer of 1954, the parents and the F_1 were grown in the experimental garden along with several F_2 and backcross progenies. The analysis of the data obtained from the measurements and observations of these progenies constitutes the basis for this report.

Measurements were made of leaf blade length and width, lobe depth and petiole diameter. For male and female flowers the following measurements were obtained: length of corolla, corolla limb, sepal, style plus stigma, staminal column, and ovary length and diameter. Other measurements included fruit length and diameter and length and diameter of several typical seeds. Fruit color, rind hardness, fruit construction, flesh color, and placenta type were also recorded.

The large sprawling plants of most species of *Cucurbita* require extensive space to mature. For this reason it is impractical to raise by conventional methods the number of plants required for a convincing genetical analysis. A more practical method of analysis adapted to the data obtained from this study was suggested by Anderson (1949, 1954), and is the method used herein. Using this method several key characters are chosen for measurement and study, exercising care to select those characters that best represent the differences between the species. Frequency distributions of the scores of each character will indicate in graphical fashion whether the two species overlap in a particular character. More effective in demonstrating the pattern of variation between species is the hybrid index which can be computed from these data. It is designed to show variation of several characters simultaneously. Such an analysis has the advantage of sharply displaying the pattern of differences and resemblances between species, and at the same time suggests how some of the characters that differentiate species are inherited. Stebbins and Ferlan (1956) used this

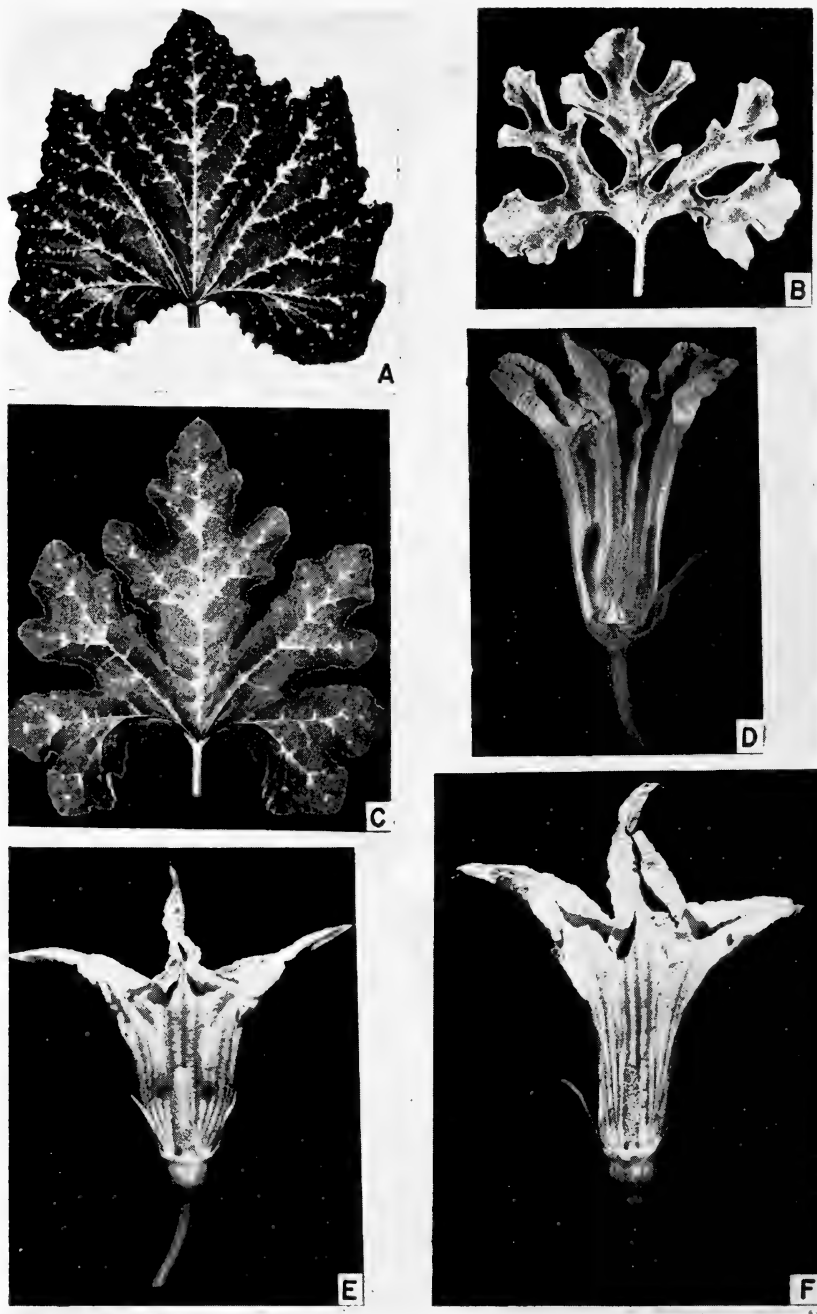


FIG. 1. Leaves and flowers of *C. lundelliana*, *C. moschata*, and F_1 hybrid.

method for investigating the role of hybridization in the origin of intra-specific polymorphism in *Ophrys*, where direct genetic experiments are not feasible for various reasons.

RESULTS

DESCRIPTION OF CHARACTERS USED IN DEVELOPING THE HYBRID INDEX. To treat the measurement and observational data in an objective manner, seven characters were arbitrarily selected for analysis. A hybrid index was computed from data similar to those recorded in Table 1 for the parents. In calculating the values for the hybrid index equal weight was arbitrarily assigned to each character. The character expressions are described as follows.

1. Leaf length / lobe depth. In *C. lundelliana* the leaves are deeply lobed (fig. 1B) as contrasted with the shallow-lobed leaves of *C. moschata* (fig. 1A). This difference is reflected in proportionately larger ratios as the leaf approaches the unlobed condition. The ratios for *C. lundelliana* range from 1.92 to 2.67; those for *C. moschata* from 5.00 to 10.60; and those for the F_1 from 3.00 to 9.00.

2. Leaf width. The leaves of *C. lundelliana* are generally much narrower than those of *C. moschata*. Leaves of *C. lundelliana* range in width from 11.5 to 15.0 cm; those of *C. moschata* from 15.5 to 31.5 cm; and those of the F_1 from 13.0 to 20.5 cm.

3. Petiole. The petioles of *C. lundelliana* are slender and reed-like, while those of *C. moschata* are stouter and more rigid. A measure of this difference is the diameter of the petiole at the point of attachment to the stem. Petiole diameter in *C. lundelliana* ranges from 0.2 to 0.4 cm; in *C. moschata* from 0.7 to 1.0 cm; in the F_1 from 0.4 to 0.6 cm.

4. Length δ corolla / length φ corolla. In *C. lundelliana* the corollas of the pistillate flowers are usually somewhat longer than those of comparable staminate flowers on the same plant, while in *C. moschata* the corollas of the pistillate and staminate flowers are about equal in length. The ratios for *C. lundelliana* range from 0.41 to 0.80; for *C. moschata* from 0.84 to 1.45; and for the F_1 hybrid from 0.57 to 1.00.

5. Fruit length / fruit width. The fruit of *C. lundelliana* is short and ellipsoidal to almost round (fig. 2A), while that of *C. moschata* is long, slender, with an enlarged terminal portion containing the seed cavity (fig. 2B). Fruits of the F_1 are phenotypically very different from those of the parents and have a constricted neck portion (fig. 2C).

FIG. 1. Leaves and flowers of *C. lundelliana*, *C. moschata*, and F_1 hybrid. A, leaf of *C. moschata* with shallow lobes and stout petiole; B, leaf of *C. lundelliana* with deep finger-like lobes and slender petiole with long hairs; C, leaf of F_1 , which appears to be about intermediate between the two species; D, staminate flower of *C. moschata*, which has short, broad corolla lobes, broad flat sepals, and a stout pedicel; E, staminate flower of *C. lundelliana*, with long, pointed corolla lobes, slender, thread-like sepals, and goblet-shaped calyx tube with slender pedicel; F, staminate flower of F_1 , which has the long, lobed corolla, slender sepals and the goblet-shaped calyx of *C. lundelliana* but has a relatively stout pedicel, $\times 0.48$.

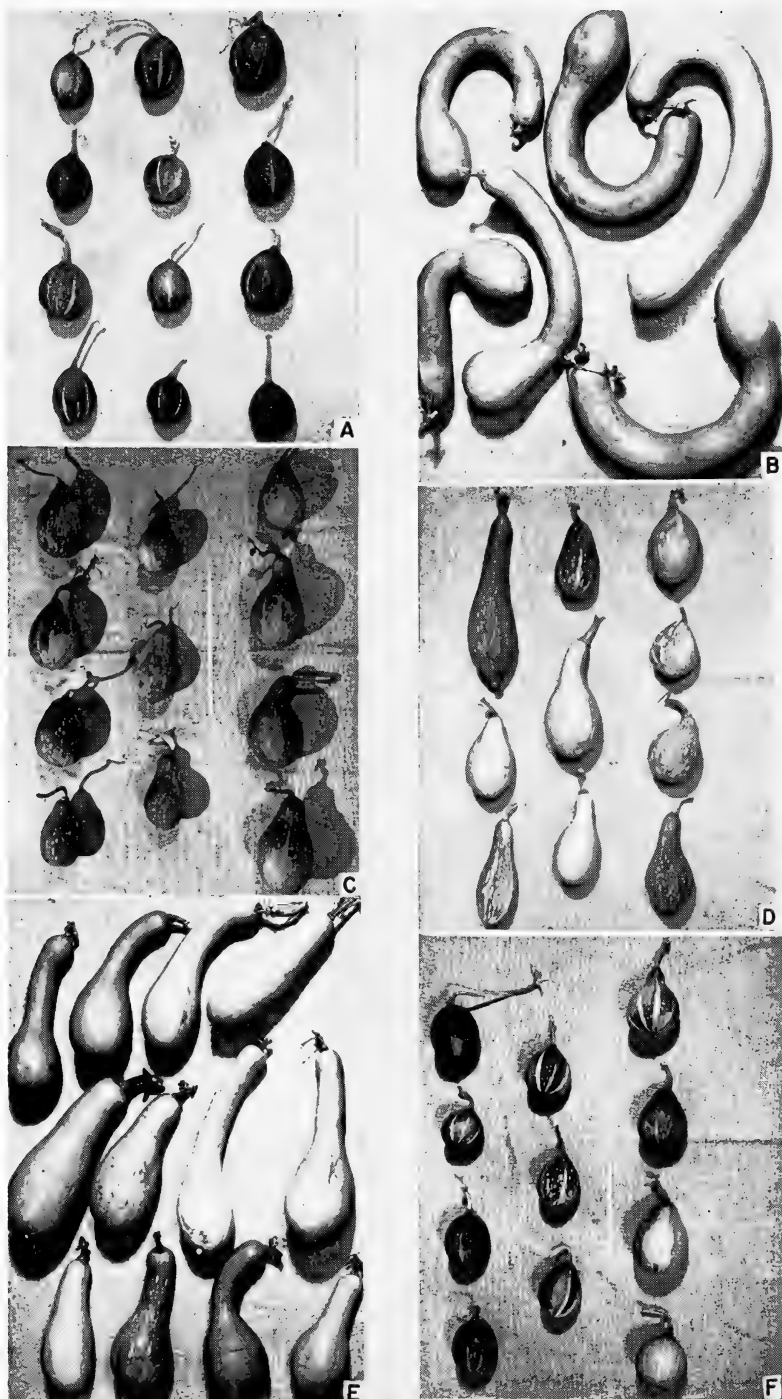


FIG. 2. Fruits of parents and progenies of *C. lundelliana* X *C. moschata*. A, *C. lundelliana*; B, *C. moschata*; C, F₁; D, F₂; E, F₁ backcrossed to *C. moschata*; F, F₁ backcrossed to *C. lundelliana*.

TABLE 1. DATA USED IN COMPUTING AND CONSTRUCTING THE HYBRID INDEX FROM SIX CHARACTERS FOR *C. LUNDELLIANA* AND *C. MOSCHATA**

Species and plant no.	Leaf length	Leaf width (cm)	Petiole diameter (cm)	Length ♂	corolla	Fruit length	Seed area (sq. cm)	Index value
	Lobe depth			Length ♀	corolla	Fruit width		
<i>C. lundelliana</i>								
5-1	2.56	11.5	0.4	0.71		1.15	0.5	1
5-2	2.27	14.0	0.3	0.64		1.08	0.5	1
5-3	2.17	13.5	0.4	0.54		1.15	0.5	0
5-4	2.36	13.5	0.4	0.52		1.13	0.5	0
5-5	1.92	14.5	0.4	0.41		1.07	0.5	1
5-6	2.67	12.5	0.3	0.52		1.13	0.5	1
5-7	2.60	13.0	0.3	0.50		1.19	0.5	0
5-8	2.27	12.0	0.3	0.60		1.00	0.5	0
5-9	2.50	13.0	0.3	0.63		1.08	0.5	1
5-10	2.50	11.5	0.2	0.75		1.07	0.5	1
5-11	2.33	15.0	0.4	0.58		1.06	0.5	1
5-12	2.30	13.0	0.3	0.80		1.07	0.5	1
<i>C. moschata</i>								
24-1	6.43	15.5	0.8	1.11		4.96	2.0	13
24-2	7.40	21.0	0.7	0.96		6.35	2.0	14
24-3	6.75	30.5	1.0	1.09		7.72	2.0	14
24-4	6.43	25.5	0.7	0.86		4.79	2.0	13
24-5	5.38	25.0	0.8	0.84		4.58	2.0	13
24-6	6.43	24.5	0.7	0.91		5.71	2.0	14
24-7	7.67	26.0	0.8	0.88		6.83	2.0	13
24-8	7.00	23.0	0.7	1.04		5.14	2.0	14
24-9	5.78	31.5	1.0	1.00		7.36	2.0	14
24-10	5.00	25.0	0.8	1.45		6.92	2.0	13
24-11	10.60	30.0	0.8	1.00		5.63	1.5	13
24-12	10.20	28.0	0.7	1.31		5.96	2.0	14

* The seventh character used in computing the hybrid index is not included in the table, since all fruits of *C. lundelliana* have hard rinds and solid placenta, while those of *C. moschata* are non-hard and non-solid. In computing the hybrid index all characters were arbitrarily given equal weight. Each individual was assigned one of three scores for each of the 7 characters; 0=similar to *C. lundelliana*; 2=similar to *C. moschata*; 1=intermediate. Employing this scheme, "pure" *C. lundelliana* =0, while "pure" *C. moschata* =14.

6. Hardness of rind and type of placenta. These two qualitative characters have been combined in the hybrid index. Fruits of *C. lundelliana* have hard, woody rinds that do not decay readily and cannot be cut with an ordinary knife. The seeds are embedded in the solid placenta (fig. 3A, right). *Cucurbita moschata* has a relatively soft rind that can be cut easily even at full maturity, while the placenta is loose and stringy and collapses at maturity leaving a large cavity (fig. 3A, left). The F_1 hybrid (fig. 3A, center) has a hard rind and a more or less open placenta.

7. Seed area. *Cucurbita lundelliana* has relatively small seeds with an area of about 0.5 sq. cm. for each seed (fig. 3B, bottom); *C. moschata* has much larger seeds with an area of about 2.0 sq. cm. per seed (fig. 3B, top). Seeds of the F_1 are about intermediate in area; they range from 0.65 to 1.35 sq. cm. (fig. 3B, center).

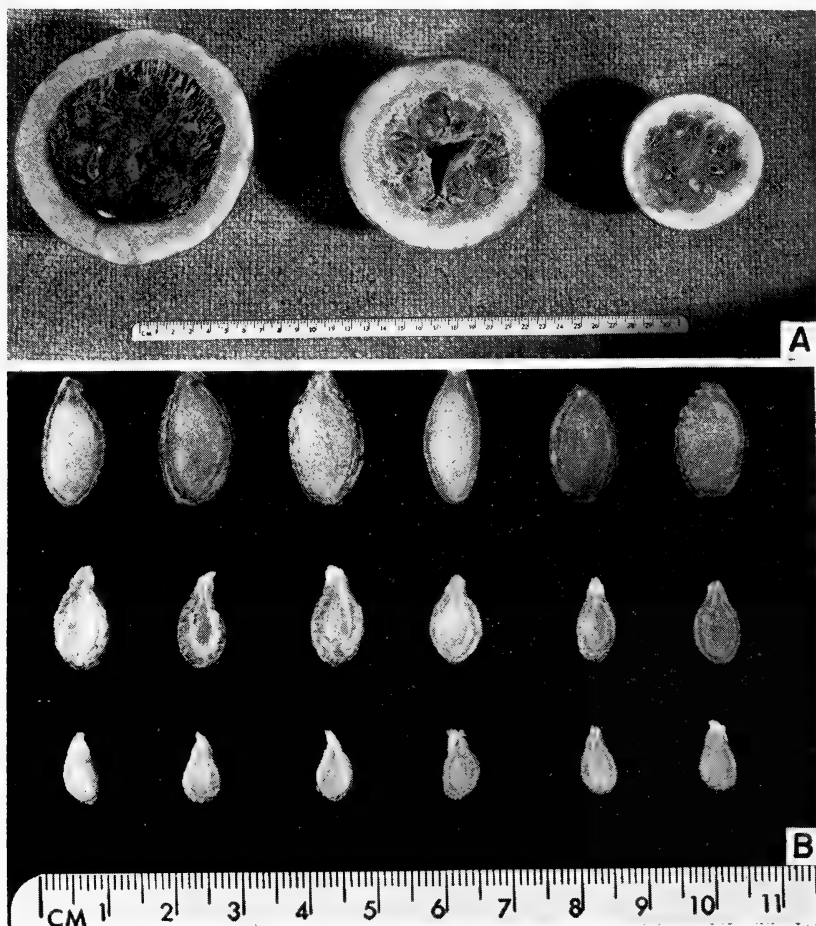


FIG. 3. A, cross sections of fruits of *C. moschata* (left), F_1 hybrid (center), *C. lundelliana* (right); B, seeds of *C. moschata* (top), F_1 hybrid (center), *C. lundelliana* (bottom).

DESCRIPTION OF THE F_1 . The F_1 plants were vigorous and thrifty and had foliage somewhat darker green than either parent. An occasional plant in the F_1 progenies had abnormal leaves and stems. Such plants died before producing flowers or maturing fruits. Of the total population of 28 F_1 plants, 7 were male-sterile. The male-sterile plants produced neither abortive nor male flowers. The F_1 plants were approximately intermediate between those of the two species in most characters (see figs. 1 and 2). The frequency distribution of hybrid index values (fig. 4) indicates a minimum overlapping of the F_1 into either species in the characters selected for analysis. There was a wide variation in pollen fertility ranging from 17 to 74%, with a mean of 42% for the 17 plants sampled.

TABLE 2. FERTILITY OF PARENTS, F₁, F₂, and BACKCROSSES OF CUCURBITA LUNDELLIANA X C. MOSCHATA

Parent or progeny	Total plants (number)	♀ -Sterile plants (number)	♂ -Sterile plants (number)	Pollen fertility	
				Mean (percent)	Range (percent)
<i>C. lundelliana</i>	12	0	0	96	85-99
<i>C. moschata</i>	12	0	0	93	80-99
F ₁	28	0	7	42	17-74
F ₂	27	1	8	39	10-74
Backcross to <i>C. lundelliana</i>	72	4	0	76	6-88
Backcross to <i>C. moschata</i>	67	0	2?	48	9-94

DESCRIPTION OF THE F₂. The bulk of the F₂ segregates were more nearly comparable with *C. lundelliana* than with *C. moschata*. In fact, for most characters the F₂ scarcely exceeded the F₁ in the direction of *C. moschata* in our sample of 27 F₂ plants. This conclusion is substantiated by the histogram of the hybrid index values (fig. 4). The different sizes and shapes of fruit produced by the segregates are shown in figure 2D. There were 8 male-sterile plants in the population of 27 plants from 4 progenies. The F₂ segregates were characterized by a wide range in pollen fertility (10 to 74%; mean 39%).

DESCRIPTION OF BACKCROSSES. The most noticeable feature of the backcross progenies was their phenotypic similarity to the recurrent parent. In general this was true of vine, flower, and fruit characters. The photographs of the fruits (figs. 2E and 2F) illustrate this point very nicely. The frequency distributions of the hybrid index values (fig. 4) suggest that the population from the backcross to *C. moschata* is more variable than that from the backcross to *C. lundelliana*. Superficially the backcrosses looked as if they might have been slightly more variable populations of either parent.

FERTILITY OF PARENTS AND PROGENIES. For the purpose of this study it was important to know something about the fertility of the individuals comprising the F₁, F₂, and backcrosses. Table 2 summarizes the data obtained from field observations and pollen counts.

The data of Table 2 indicate that about one quarter of the F₁ and F₂ individuals from the cross are male-sterile. Plants which did not produce male flowers and those which produced male flowers but aborted prior to anthesis were lumped in this category. It is worth noting that there was not a single clear-cut case of male sterility in the backcross progenies. One plant in the F₂ and 4 plants in the backcross to *C. lundelliana* were males; that is, no female flowers were produced. The pollen fertility of the parent species is very nearly identical (mean 93 and 96%), while the means of the F₁ and F₂ are not very different (42 and 39%). On the other hand the mean pollen fertility for the backcross to *C. lundelliana* was 76% (range 6 to 88%) and that for the backcross to *C. moschata* was only 48% (range 9 to 94%). This sharp difference in mean fertility be-

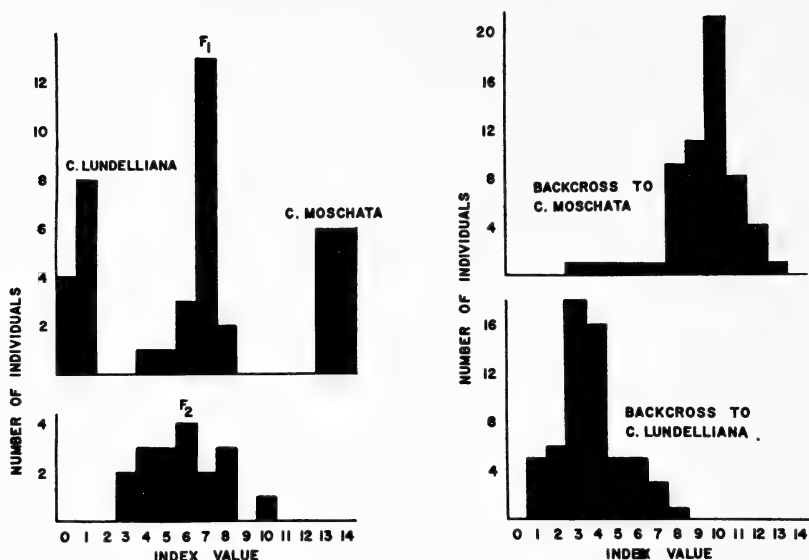


FIG. 4. Frequency distributions of hybrid index values for *Cucurbita lundelliana*, *C. moschata*, their F_1 , F_2 , and backcross progenies to both parent species (further explanation in the text).

tween the backcross progenies suggests that maternal or cytoplasmic factors are effective in restoring to a marked degree the pollen fertility of the progenies of the backcross to the maternal parent.

DISCUSSION

The method of analysis chosen for this study has many shortcomings, but it does illustrate certain characters by which the two species differ, and gives a rough quantitative measure of these differences.

The data suggest that some fruit characters, such as large size, soft rind, highly colored flesh, and large seeds, which presumably have value under cultivation, are for the most part recessive. On the other hand, vegetative and flower characters, which in this instance appear to be of less importance under domestication, are intermediate in their expression.

Although the backcross progenies are remarkably similar to the recurrent parent in fruit characters, the frequency distribution of the hybrid-index values (fig. 4) suggests that genes of the other parent are present. The subtle nature of this hereditary contribution cannot be detected except by careful study.

The frequency distribution of the hybrid-index values (fig. 4) indicates that while the F_2 values were considerably more variable than the F_1 , as would normally be anticipated, they did not reach values of either of the parent species in the population sampled. The backcross to *C. lundelliana* extends up to the modal class of *C. lundelliana*. However, its own mode is about halfway between the *C. lundelliana* mode and the F_1 mode.

The backcross to *C. moschata* barely reaches the mode of *C. moschata*, and again its mode is approximately halfway between those of the recurrent parent and the F_1 .

SUMMARY AND CONCLUSIONS

1. Controlled pollinations demonstrated that a wild annual species of *Cucurbita* (*C. lundelliana*) can exchange genes with a cultivated species (*C. moschata*). The F_1 is fertile enough to produce F_2 and backcross progenies. Individuals of these progenies are fertile in varying degrees except for some male sterility in the F_1 and F_2 generations and for one backcross progeny that had at least 4 individuals that were female-sterile.

2. The parent species are well separated by differences in important morphological characters. This separation is illustrated by frequency distributions constructed from hybrid-index values. From the frequency distributions it is evident that of the 7 characters selected for analysis none are overlapping. The F_1 is intermediate between the parents in the characters selected for analysis except for the qualitative characters—rind hardness and placenta type. An analysis shows that in most characters, the F_2 population barely exceeds the F_1 in the direction of *C. moschata*. This analysis combined with a similar analysis of the backcross progenies suggests that *C. moschata* has many recessive genes.

3. Comparisons of the backcross progenies indicate that they are strikingly similar to the recurrent parent in appearance. This finding suggests that various isolating barriers such as linkage, selective fertilization, and differential viability affect the backcross.

4. If compatibility relations are used as criteria, the isolating barriers that prevent crossing between *C. lundelliana* and *C. moschata* are not well developed in spite of the great morphological diversity between the species. There seems no doubt that each species is a good taxonomic entity. It is equally clear that the two species have a number of genes in common. For this reason it is not unreasonable to suggest that *C. moschata* may have been derived from *C. lundelliana* by isolation and subsequent selection by man. An alternative suggestion would be that both species were derived from a common ancestor, but when domesticated, *C. moschata* diverged sharply by natural selection under the guidance of man.

U. S. Department of Agriculture
Agricultural Research Service
Crops Research Division
La Jolla, California

LITERATURE CITED

- ANDERSON, E. 1949. Introgressive hybridization. *Biol. Reviews* 28:280-307.
———. 1954. Efficient and inefficient methods of measuring specific differences. *Statistics and Mathematics in Biology*. pp. 93-106. Iowa State College Press. 1954.
STEBBINS, G. LEDYARD AND L. FERLAN. 1956. Population variability, hybridization, and introgression in some species of *Ophrys*. *Evolution* 10:32-46.
WHITAKER, THOMAS W. 1956. The origin of the cultivated *Cucurbita*. *Amer. Nat.* 90:171-176.

THE REPRODUCTIVE STRUCTURES OF SCHINUS MOLLE (ANACARDIACEAE)

HERBERT F. COPELAND

The *Vergleichende Embryologie der Angiospermen* of Schnarf (1931) has served as the basis and stimulus for very extensive subsequent work in its field. Schnarf accounted for the Anacardiaceae on the basis essentially of a single paper dealing with a single species, being the account of *Rhus Toxicodendron* L. (or *Toxicodendron radicans* O. Kuntze) by Grimm (1912). Subsequent studies of floral morphology and embryology in this family include the following: Juliano (1932) on *Spondias purpurea* L.; Juliano and Cuevas (1932) on *Mangifera indica* L.; Maheshwari (1934) on *Mangifera indica*; Srinivaschar (1940) on *Semecarpus Anacardium* L., *Spondias Mangifera* Willd., and *Anacardium occidentale* L.; Copeland and Doyel¹ (1940) on *Toxicodendron diversilobum* Greene; Sharma (1954) on *Mangifera indica*; Copeland² (1955) on *Pistacia chinensis* Bunge; Kelkar (1958a) on *Rhus mysurensis* Heyne; and Kelkar (1958b) on *Lannea coromandelica* (Houtt.) Merrill. The present paper adds *Schinus Molle* L. to the list of species of Anacardiaceae in which the morphology of the reproductive structures is reasonably well known.

Material was collected in the public parks of the City of Sacramento and prepared by routine microtechnical methods (a special technique applied to pollen grains is described below). The results fall short of desired completeness in failing to account for the growth of the pollen tube and for fertilization.

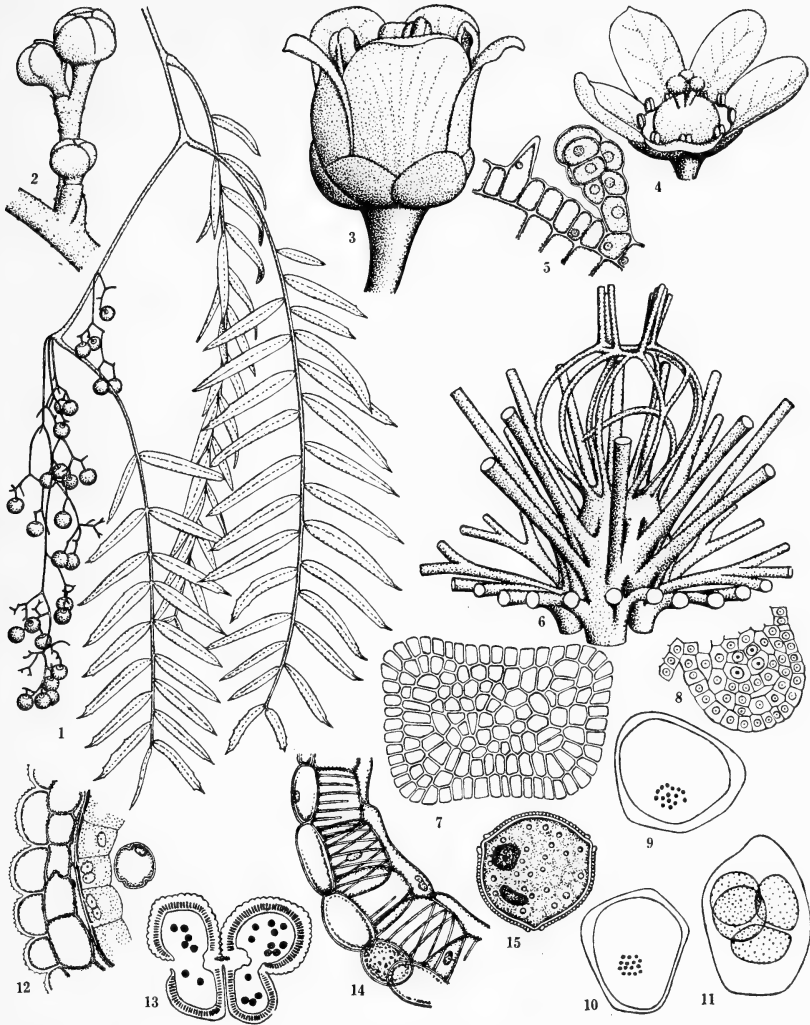
THE TREE

Braunton and Davy (1914) tell us that *Schinus Molle* is a native of Peru; that its common name is Peruvian mastic; and that it is very familiar as a cultivated ornamental in southern California, where it has the common name of pepper tree. It is in fact familiar also in northern California, and in many other moderately warm countries.

The tree is fast-growing; of deliquescent form; rarely much more than 10 m. tall; evergreen, with alternate pinnate leaves, the branchlets and leaves often pendant; the small yellow flowers abundant in terminal clusters; dioecious; the female trees producing bunches of purplish-red

¹ Bernice Elva Doyel, afterward Mrs. Harold Strimling, my pupil, associate, and friend, died in Sacramento on February 24, 1954, at the age of 34 years.

² It behooves me to acknowledge, and to call to the attention of readers, a ludicrous error in the paper cited. The median stigma of *Pistacia* is said to stand above the large end of the ovary, in which the ovule is attached. Actually it stands above the small end. Referring to a passage in this paper in the second column of page 442, figures 17, 18, 19, 20, and 21 were drawn with the median stigma to the right; my other figures of the gynoecium and its parts were drawn with the median stigma to the left.



FIGS. 1-15. *Schinus Molle*: 1, fruiting twig, $\times 0.4$; 2, cluster of flower buds, $\times 8$; 3, male flower, $\times 8$; 4, female flower, $\times 8$; 5, pubescence of pedicel, $\times 320$; 6, model of the vascular system of a female flower, $\times 40$; 7, cross section of young anther, $\times 320$; 8, cross section of one lobe of an older anther, $\times 320$; 9, 10, heterotypic metaphase in pollen mother cell, $\times 720$; 11, microspore tetrad, $\times 720$; 12, cross section of wall of developing anther, $\times 320$; 13, cross section of mature anther, $\times 40$; 14, portion of cross section of mature anther, $\times 320$; 15, pollen grain, $\times 720$.

drupes about 5 mm. in diameter (fig. 1). It was the odor and taste of these fruits that suggested the common name of pepper tree.

The pepper tree has not the typical reproductive cycle of plants of temperate regions. It produces flowers continually from spring to fall. It

responds to the approach of winter by dropping its flower buds, flowers, and young fruits, and by ceasing to grow until the following spring.

In Sacramento, some of the minute axillary buds give rise to branches at about the beginning of the month of March. Each branch bears first two minute alternate scales, these being the covering of the bud. The axis of the branch elongates during a period of from six to eight weeks, producing from three to seven or more foliage leaves. The terminal bud then produces an inflorescence, or else dies: terminal buds do not normally serve as winter buds. Flowers appear first on a particular tree from the middle of May to the middle of June. They are evidently entomophilous, and honey bees have been seen to visit them. Fruits are mature about two months after flowering: the first ones of the year are found at about the beginning of August.

The axis of a flower cluster, continuing that of a branch, grows in indeterminate fashion, bearing a series of alternate scales, but eventually producing a terminal flower. From the axil of each scale grows an axis bearing, ordinarily, two scales and a terminal flower; from the axils of these scales, in basipetal succession, further growth takes place, usually of a single flower, sometimes of a further cluster (fig. 2). The entire cluster of flowers as described is identifiable as a thyrses.

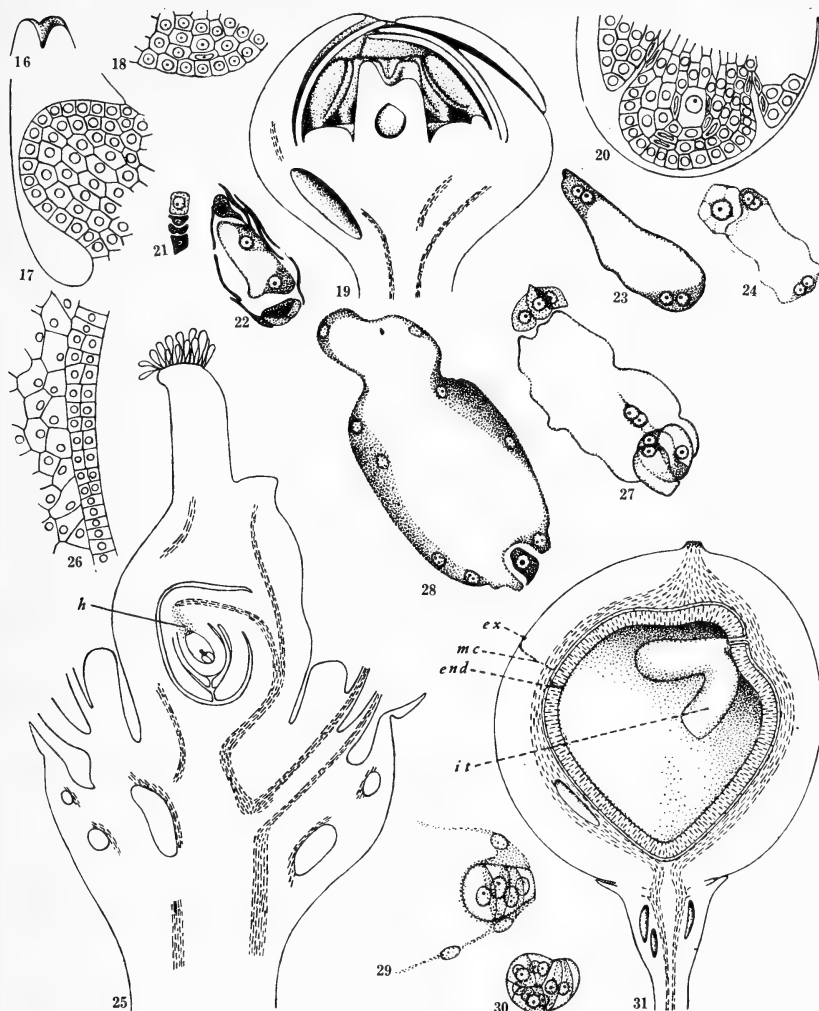
The plant as a whole appears glabrous, but there is a scant pubescence of glandular and simple hairs on the axes and scales of the inflorescence (fig. 5).

FLOWERS

The male flowers (fig. 3) are slightly larger, and have more erect petals, than the female (fig. 4). Each flower has five sepals, five petals, ten stamens, and a pistil. A prominent disk surrounds the base of the ovary inside the bases of the stamens. A small number of stomata are present in its epidermis. The male flowers have minute and incompletely developed pistils; the female flower bear smaller stamens than the male. The sporogenous cells in the anthers of female flowers undergo abortion at the stage of pollen mother cells.

The mature pistil of the female flower is dorsiventral, but not conspicuously so: in the microtechnical operation of imbedding pistils with the intention of cutting sagittal sections, one makes a considerable number of mistakes. The ovary is of a shape approaching that of an egg laid upon its side: it has a larger and a smaller end; a brief style with a terminal stigma stands in a median position toward the smaller end of the ovary; two lateral styles with their stigmas, not particularly different from the median one, stand above the larger end. As a fairly frequent abnormality, pistils occur with only two styles, one above each end. The ovary contains a single locule almost entirely filled by the single ovule. This is attached to the ovary wall in the median plane of the ovary, at the large end, above the middle (fig. 25).

In the phloem of every vascular bundle, but not extending to the ex-



FIGS. 16-31. *Schinus Molle*: 16, longitudinal section of ovary in young female bud, $\times 40$; 17, beginning of development of ovule, $\times 320$; 18, beginning of periclinal division in the nucellar hypodermis, $\times 320$; 19, longitudinal section of female flower bud, $\times 40$; 20, megaspore mother cell, $\times 320$; 21, tetrad of megaspores, $\times 320$; 22, 2-nucleate embryo sac, $\times 320$; 23, 4-nucleate embryo sac, $\times 320$; 24, an abnormality, an embryo sac developing from the spore next to the chalazal spore, $\times 320$; 25, longitudinal section of female flower with a mature embryo sac, $\times 40$; 26, inner epidermis of ovary of open flower, $\times 320$; 27, mature embryo sac, $\times 320$; 28, undivided zygote in plurinucleate endosperm, $\times 320$; 29, 30, young embryos, $\times 320$; 31, longitudinal section of fruit about one month after anthesis, $\times 8$. *h*, hypostase; *it*, tubular outgrowth of outer integuments; *ex*, exocarp; *mc*, mesocarp; *end*, endocarp.

treme end of the bundle, there is a resin duct, conspicuous under the microscope, being of greater bulk than the vascular tissues. The resin ducts enable one easily to follow the course of the bundles.

About five bundles, arranged in a cylinder, ascend the pedicel and enter the receptacle. In the base of the receptacle they fuse and fork to a certain extent, and send out in radial directions branches which undergo further forking. These are the sepal supply; about five bundles enter each sepal. Above their departure, the stele sends out three successive alternating whorls of five bundles, supplying respectively the petals, the sepalad stamens, and the petalad stamens. In male flowers, the vascular tissue ascending beyond the departure of the stamen traces is scant and quickly fades out. In female flowers (fig. 6), much vascular tissue ascends beyond this point. It is of the form of a truncate cone splitting at the summit to form a whorl of bundles whose typical number is eight. One ascends the small end of the ovary; two ascend each side; at the large end there are typically two ovary wall bundles, and between them, or, often, fused to one of them, the bundle which supplies the ovule. At the summit of the ovary, the ovary wall bundles meet and form a scant network. From this network, branches go up into the styles, each style receiving a median bundle and two laterals.

MALE STRUCTURES

The stamens are in all respects of the structure typical of flowering plants. Within the four angles of the rudimentary anther (fig. 7), periclinal divisions occur in the hypodermal cells. The progeny of these cells, produced by duly numerous divisions, become differentiated into the following layers of the anther, in order from outward to inward: (a) the endothecium, the hypodermal layer of cells with ribbed walls, whose contraction opens the anther through two longitudinal clefts (figs. 13, 14); (b) two layers of wall cells, of which the outer becomes compressed, and the inner crushed and absorbed (figs. 12, 14); (c) a tapetum of the secretion type, the cells becoming binucleate and then shrivelling and disappearing (fig. 12); and (d) the spore mother cells. In the male flower, meiosis duly takes place within these last. The haploid chromosome number, observed during this process, is 15 (figs. 9, 10). The pollen grains are separated by simultaneous furrowing. The mature pollen grain (fig. 15) has a wall marked by numerous fine pits and three meridional grooves.

The pollen grains contain much stainable material, and it has been difficult to be certain of the number of nuclei. A technique by which they were made visible was as follows: microtome sections, mounted, deparaffined, and hydrated, were exposed for 20 minutes to 1% Na_2CO_3 to which a little NaOH had been added, at $60^\circ\text{C}.$; stained briefly with methylene blue; and destained in 95% alcohol. Two nuclei are present. The tube nucleus is the larger. It is subglobular and contains a visible nucleolus. The generative nucleus is smaller, fusiform, and heavily staining. It lies within a distinct space, the generative cell

THE OVULE

The parts of the flower originate in the bud in acropetal succession. The pistil, in the female bud, originates as a cycle of three knobs, evidently rudimentary carpels, which, as they grow, become coalescent at the base (fig. 16). Somewhat above the bottom of the cavity in the resulting three-pointed cone, the nucellus begins to grow into it from an area below one of the notches between the points (fig. 17). By further growth, the ovary becomes closed above the locule containing the developing ovule (fig. 19). The points above develop, of course, into the styles and stigmas.

The direction of the axis of the nucellus is at first horizontal or slightly upward. It soon bends and grows diagonally downward. At about this time, the inner integument originates as a collar of tissue surrounding the tip of the nucellus and growing forward with it. The hypodermal cells of a small area near the tip of the nucellus begin to undergo periclinal divisions. One of these cells, near the middle of the area, cuts off to the inside a cell, slightly larger than the others, which is to become the megaspore mother cell (fig. 18). By further periclinal divisions, the megaspore mother cell is carried well to the interior of the nucellus (fig. 20); by growth in other parts, an outer integument is produced; both integuments extend beyond the nucellus and close over it, leaving a small micropyle. At the same time that the growth of the ovule produces these changes, it continues to have a bending or coiling effect: the mature ovule is so bent that its axis points to the ovary wall below its insertion (fig. 25).

Meanwhile, the spore mother cell has produced a tetrad of spores (fig. 21), among which the chalazal spore is functional. The nucleus of the functional spore undergoes three divisions (figs. 22, 23). Six of the resulting eight nuclei are set apart in an egg, two synergids, and three antipodal cells, leaving two polar nuclei in the endosperm mother cell (fig. 27). Thus the embryo sac is of the type which Schnarf designated as normal.

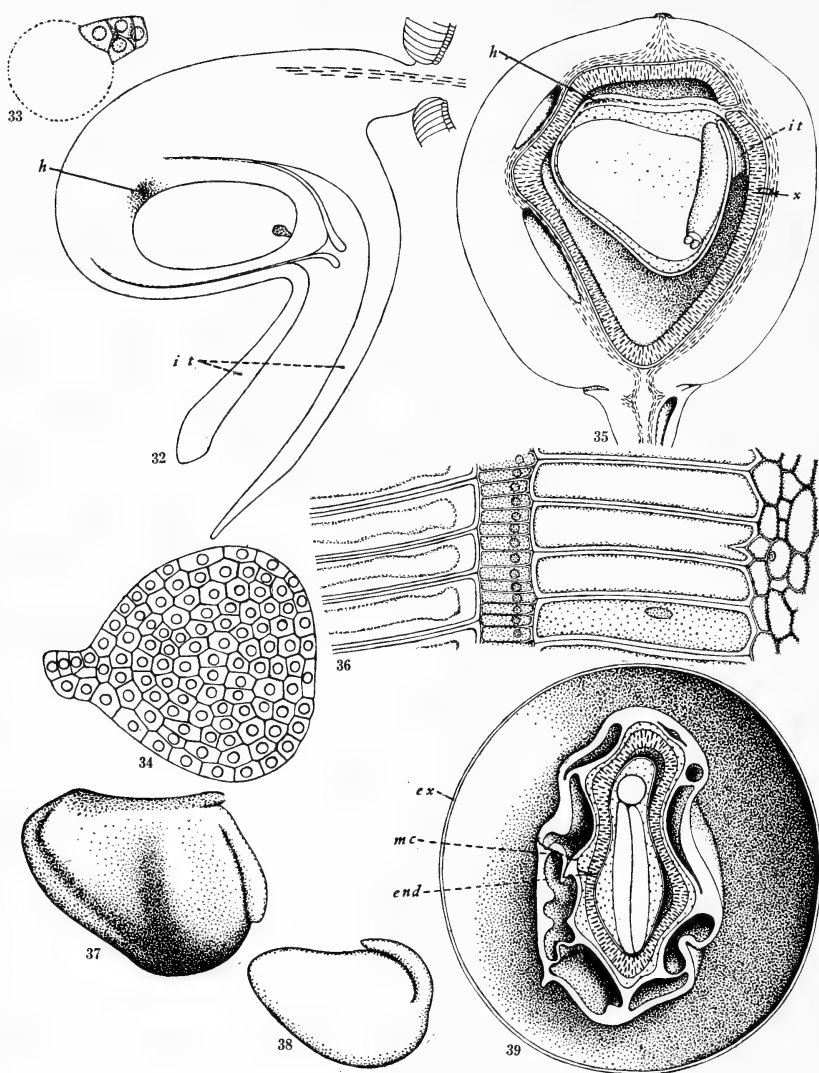
As the embryo sac approaches maturity, there appears in the chalaza, between the end of the bundle traversing the raphe and the antipodal cells, a hypostase (figs. 25, 32, 35), being a body of thick-walled cells of moribund appearance.

A few examples of abnormal development have been noted. An occasional ovule is distorted, twisted otherwise than in the normal downwardly coiled fashion. Sometimes a megaspore other than the chalazal one undergoes development (fig. 24).

DEVELOPMENT OF FRUIT AND SEED

The ovary grows during about four weeks after anthesis approximately to the full size of the fruit (fig. 31).

At anthesis, the cells of the inner epidermis of the ovary show periclinal divisions (fig. 26). By these divisions, the epidermis gives rise to three regular layers of cells. The cells of the innermost layer become radially elongate to a length of about 0.2 mm., after which they develop thick



FIGS. 32-39. *Schinus Molle*: 32, longitudinal section of ovule about one month after anthesis, $\times 40$; 33, 34, developing embryos, $\times 320$; 35, longitudinal section of nearly mature fruit, $\times 8$; 36, section of endocarp, area *x* of fig. 35, $\times 320$; 37, mature seed, $\times 8$; 38, mature embryo, $\times 8$; 39, cross section of mature fruit, $\times 8$. *h*, hypostase; *it*, tubular outgrowth of outer integument; *ex*, exocarp; *mc*, mesocarp; *end*, endocarp.

walls. The middle layer becomes a palisade of thin-walled cells, very much smaller than the preceding. The outer becomes a palisade of thick-walled cells, of about the diameter of those of the inner layer, but only about 0.05 mm. long (fig. 36). These three layers, all derived from the

inner epidermis of the ovary, make up the stony endocarp of the fruit. Until about a month after anthesis, it is possible to cut on the microtome paraffin sections of the endocarp; later, the thickness and hardness of the walls make this impossible. The endocarp is deeply impressed by the meridional bundles, with their large resin ducts, in the ovary and fruit. As compared with the more or less egg-shaped ovary and fruit, the endocarp is more strongly compressed in the lateral dimension, being approximately lenticular.

During the first month after anthesis, the ovule grows principally in its micropylar-chalazal dimension. The shape of its axis becomes that of a horizontal U: the end of the nucellus points to an area directly below the insertion of the ovule. The outer integument grows forth as a prominent tube, directed downward in the large end of the ovary at right angles to the rest of the ovule. This structure is presumably without function (figs. 31, 32). It persists in a shrivelled condition in the mature fruit (figs. 35, 37).

The endosperm is of nuclear type. It contains a considerable number of free nuclei before the zygote divides (fig. 28). The nuclei remain free when the embryo is 4-celled (fig. 29); when the embryo is of about a dozen cells (at the stage shown in fig. 30), cellular endosperm has begun to form about it. Further uninucleate cells are cut out, first throughout the surface of the endosperm, and then throughout its interior.

The first division of the zygote has not been seen. It occurs about three weeks after anthesis, and is believed usually to be by an oblique wall. The epibasal cell divides, by walls which are usually oblique, two or three more times. Longitudinal divisions then begin, first in the more distal cells, then in the more proximal, but not usually in the basal cell. Thus when a globular embryo is formed (figs. 33, 34), it has a suspensor which is brief and not sharply set apart, consisting of a basal cell which is not enlarged and of one or two pairs of cells beyond this.

After the fruit and its locule have reached nearly their full size, the seed and embryo enter their phase of most rapid enlargement. The seed fills the locule laterally; its end toward the large end of the fruit becomes vertically elongate; it bulges greatly on the side away from the raphe. The impressions in the endocarp, produced by resin ducts, produce impressions on the sides of the seed.

The vertical elongation of the end of the seed toward the large end of the fruit is accompanied by elongation of the hypocotyl and radicle as a stout column in this end of the seed. The root tip points upward, and remains for a long time near the micropyle, but eventually grows past and curves away from it (fig. 38).

The cotyledons grow forth at right angles to the direction of the hypocotyl. They lie in planes parallel to the median plane of the fruit and seed. The raphe increases only moderately in length; the seed coat and endosperm grow forth beyond its end, and the sharp points of the cotyledons extend beyond the hypostase into the pocket thus formed.

The plumule consists of two small knobs placed decussately with respect to the cotyledons.

After the fruit and seed have reached apparent structural maturity, the mesocarp, containing the bundles and resin ducts, becomes shrivelled. A pigmented filmy exocarp, consisting of the external epidermis of the fruit together with one hypodermal layer, encloses a vacant space. Within this, the mesocarp, of gummy consistency, forms a layer on the surface of the stone. A considerable body of endosperm survives in the mature seed (fig. 39).

DISCUSSION

Here one attempts to characterize the Anacardiaceae by their reproductive structures, microscopic as well as macroscopic. Since the microscopic structures are definitely known only of a moderate number of species, most of which belong to the single tribe Rhoideae, the characterization is acknowledgedly tentative.

The Anacardiaceae bear flowers in cymes which are usually gathered into thyrses. They produce imperfect flowers, some species being dioecious, others polygamous. The imperfect flowers usually appear complete through the presence of rudimentary organs. The flowers are pentamerous, except that in most species the gynoecium is of fewer than five carpels. The ovary or ovaries are superior, surrounded at the base by a prominent disk. (To several of these statements, *Pistacia* offers exceptions, evidently through loss of parts.) In the tribe Rhoideae, the pistil is compound, consisting of one fertile and two sterile carpels, with separate styles and stigmas. There is a single locule. A single ovule is attached basally or else to the wall of the locule, on the side away from the mid-plane of the fertile carpel.

Except in the gynoecium, the receptacular vascular system is undistinguished, a matter of the stele emitting alternating whorls of bundles. The sepalad whorl of stamens is the lower. With the reduction of some of the carpels is associated the fact that the ovary wall bundles are not definitely identifiable as carpel dorsals, carpel laterals, and so forth. When the ovule is basifixed, the bundle supplying it is formed by the anastomosis of several or many bundles running together from all sides. This evidently derived character has been noted outside of tribe Rhoideae in *Mangifera* (Sharma, 1954).

Stamens and pollen show no characters distinguishing Anacardiaceae from flowering plants in general. The four pollen sacs open, by the action of a ribbed endothecium, through two slits. The tapetum is of the secretion type: the cells become and remain binucleate, and remain separate until they are absorbed. The most frequently observed haploid chromosome number is 15; Srinivasachar found 14 in *Spondias*. The pollen grains are separated by simultaneous furrowing. They are binucleate. The exine is in many examples marked by numerous fine pits and by three meridional grooves, and contain two nuclei.

Ovule and seed grow in such fashion as to become more or less strongly apotropously coiled in the median plane of the pistil. Basically, the ovule is bitegmous, but various genera exhibit peculiarities in the development of the integuments, particularly the outer. One suggests for future study the possibility that the obturator, the outgrowth at the base of the funiculus which occurs in various genera but not in *Schinus*, may be morphologically a part of the outer integument.

The ovule is crassinucellate. In the area of the tip of the nucellus, there is a hypodermal archesporium, a layer of cells which undergo periclinal divisions. Only one cell of this layer is functionally archesporial: only one megaspore mother cell is produced (these points, not established in our paper on *Toxicodendron diversiloba*, have been observed in subsequently prepared slides of this species). In the chalaza there is present a hypostase, a body of thick-walled cells of moribund appearance.

The embryo sac is of the type which Schnarf designated as normal. Current usage designates this the *Polygonum* type, a term which fails to express what we believe to be its significance.

The peculiar types of development in the integuments are believed to be associated with the occurrence of aporogamy, which is definitely known in *Toxicodendron* and *Pistacia*. Double fertilization is presumed to occur, but has been observed only in *Spondias* (Srinivasachar, 1940).

The fruit grows nearly to its full size before the ovule grows considerably, and the ovule grows considerably before the embryo does so. The occurrence of these three distinguishable cycles of growth was noted in *Mangifera* by Kennard (1955).

The fruit is a drupe. In tribe Rhoideae, the endocarp is derived entirely from the inner epidermis of the ovary: it appears regularly to consist of three definite layers of cells; its stony character is produced by the maturation of one or more of these layers as dense palisades of fiber-like cells. These things appear not to be true of *Mangifera* and *Spondias*.

The endosperm is of nuclear type. It becomes cellular first about the embryo, then throughout its periphery, then in all parts.

The first divisions of the zygote are more or less oblique. A brief suspensor, not definitely set apart, or none, is produced.

Enlargement of the ovule in the course of becoming a seed involves considerable bulging on the side describable as the lower, away from the raphe. The raphe does not elongate considerably, but the enlarging seed coat and endosperm push forth beyond the hypostase which marks the end of the raphe. As the growing seed bulges downward, elongation of the hypocotyl-radicle pushes its proximal end downward, while the root tip remains in the neighborhood of the micropyle. The cotyledons lie in planes parallel to the mid-plane of the gynoecium. They grow forth approximately at right angles to the hypocotyl, and their tips extend beyond the hypostase. A certain amount of endosperm survives in the mature seed.

We will be able to recognize other groups of plants as immediate allies of Anacardiaceae whenever we discover in them assemblages of characters showing a family resemblance to the foregoing. Observations of the same nature as these upon further Anacardiaceae should lead to improvements in the system of the family. In the present state of knowledge, it appears that *Schinus* is relatively primitive, and *Pistacia* relatively advanced.

SUMMARY

Schinus Molle, a South American tree popular as an ornamental in California, where it is called the pepper tree, is dioecious. Flowers of both sexes, produced throughout the summer in thyrses, appear complete, but in each the organs of opposite sex are imperfectly developed.

The male parts exhibit no notable peculiarities: endothecium ribbed; tapetum of secretion type, the cells becoming binucleate; haploid chromosome number 15; pollen grains 3-grooved, binucleate.

The pistil is compound, of one fertile and two sterile carpels, with separate styles and stigmas. The single locule contains a single ovule, attached to the wall on the side opposite the style of the fertile carpel. It is apotropous, bitegmous, crassinucellate. A hypodermal layer of archesporial cells in the distal end of the nucellus produces a single megaspore mother cell. The embryo sac is of normal type.

After anthesis, the ovary grows in about four weeks nearly to the size of the mature fruit; ripening requires another month. The fruit is a drupe whose exocarp, of only two layers of cells, encloses, in an empty space, a gummy mesocarp about a stony endocarp. The endocarp is derived entirely from the inner epidermis of the ovary, and consists of three layers of radially elongate cells, two of them with greatly thickened walls.

Considerable enlargement of the ovule is delayed until the fruit is nearly of its full size, and the embryo grows but little until the ovule is in full course of enlargement. The enlarging ovule is marked by a peculiar tube-like extension of the outer integument. The endosperm is nuclear. The first divisions of the zygote are oblique. The suspensor is brief and not sharply set apart from the embryo proper. In the mature seed the hypocotyl points vertically upward in the end of the seed toward the larger end of the fruit; the cotyledons project at right angles from its lower end; a certain amount of endosperm remains present.

Most of these characters are found, by comparison with those of various other Anacardiaceae, to be characters of family Anacardiaceae, or at least of tribe Rhoideae. Groups other than Anacardiaceae will confidently be recognized as related to this family when sets of characters showing a family similarity to these are observed in them.

Sacramento Junior College,
Sacramento, California

LITERATURE CITED

- BRAUNTON, E., and J. B. DAVY. 1914. *Schinus*. In Bailey, L. H., Standard Cyclopedia of Horticulture 6:3108-3109.
- COPELAND, H. F., and B. E. DOYEL. 1940. Some features of the structure of *Toxicodendron diversiloba*. *Am. Jour. Bot.* 27:932-939.
- COPELAND, H. F. 1955. The reproductive structures of *Pistacia chinensis* (Anacardiaceae). *Phytomorphology* 5:440-449.
- GRIMM, J. 1912. Entwicklungsgeschichtliche Untersuchungen an *Rhus* und *Coriaria*. *Flora* 104:309-334.
- JULIANO, J. B. 1932. The cause of sterility in *Spondias purpurea* Linn. *Philippine Agriculturist* 21:15-24.
- JULIANO, J. M., and N. L. CUEVAS. 1932. Floral morphology of the mango (*Mangifera indica* L.) with special reference to the Pico variety from the Philippines. *Philippine Agriculturist* 26:443-472.
- KELKAR, S. S. 1958a. Embryology of *Rhus mysurensis* Heyne. *Jour. Indian Bot. Soc.* 37:114-122.
- KELKAR, S. S. 1958b. A contribution to the embryology of *Lannea coromandelica* (Houtt.). *Merr. Jour. Univ. Bombay* 26:152-159.
- KENNARD, W. C. 1955. Development of the fruit, seed, and embryo of the Paheri mango. *Bot. Gaz.* 117:28-32.
- MAHESHWARI, P. 1934. The Indian mango. *Current Sci.* 3:97-98.
- SCHNARF, K. 1931. *Vergleichende Embryologie der Angiospermen*. Berlin.
- SHARMA, M. R. 1954. Studies in the family Anacardiaceae. I. Vascular anatomy of the flower of *Mangifera indica* L. *Phytomorphology* 4:201-208.
- SRINIVASACHAR, D. 1940. Morphological studies in the family Anacardiaceae. *Jour. Mysore Univ. n.s. B* 1:83-91.

DEVELOPMENT OF THE MEGAGAMETOPHYTE IN LIQUIDAMBAR STYRACIFLUA L.

FRANKLIN F. FLINT

No work has been published on the megagametophyte of *Liquidambar*. Within the family (Hamamelidaceae) only two other genera have been studied in regard to megasporogenesis and megagametogenesis (Flint, 1957, 1957A).

Pistillate floral heads of *Liquidambar styraciflua* were collected in Dinwiddie County, Virginia, from March 28 until July 10, 1953. They were fixed in formalin-aceto-alcohol in the proportions of 90 cc. of 70 percent ethyl alcohol to 5 cc. formalin and 5 cc. of glacial acetic acid. Tertiary butyl alcohol, as used by Johansen (1940), was found most satisfactory for dehydration. The heads were then embedded in tissuemat, sectioned at 10-30 microns, and stained with Harris' Hemotaxylol, Safranin O, and Fast Green FCF.

Around 245 ovules are included in this study. Ovules which showed signs of unusual plasmolysis, nuclear degeneration, or had unusually dark staining cytoplasm were eliminated and are not included in the above count.

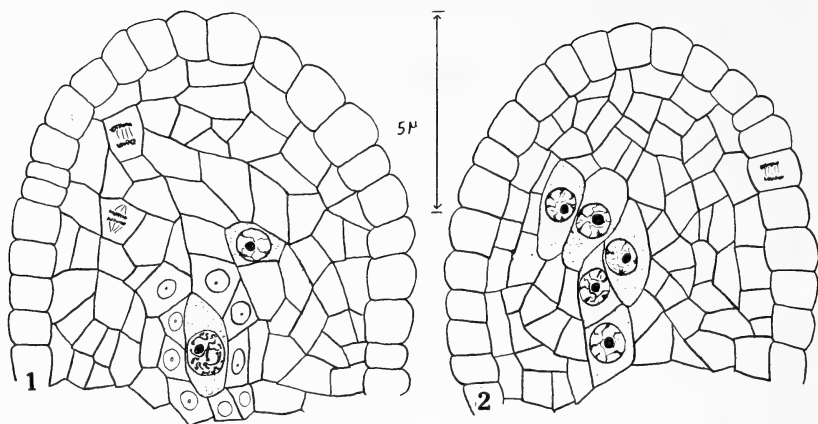


FIG. 1. Young ovule with one megaspore mother cell and one other enlarged nucellar cell. FIG. 2. Young ovule with five potential mother cells. Only one will form megaspores.

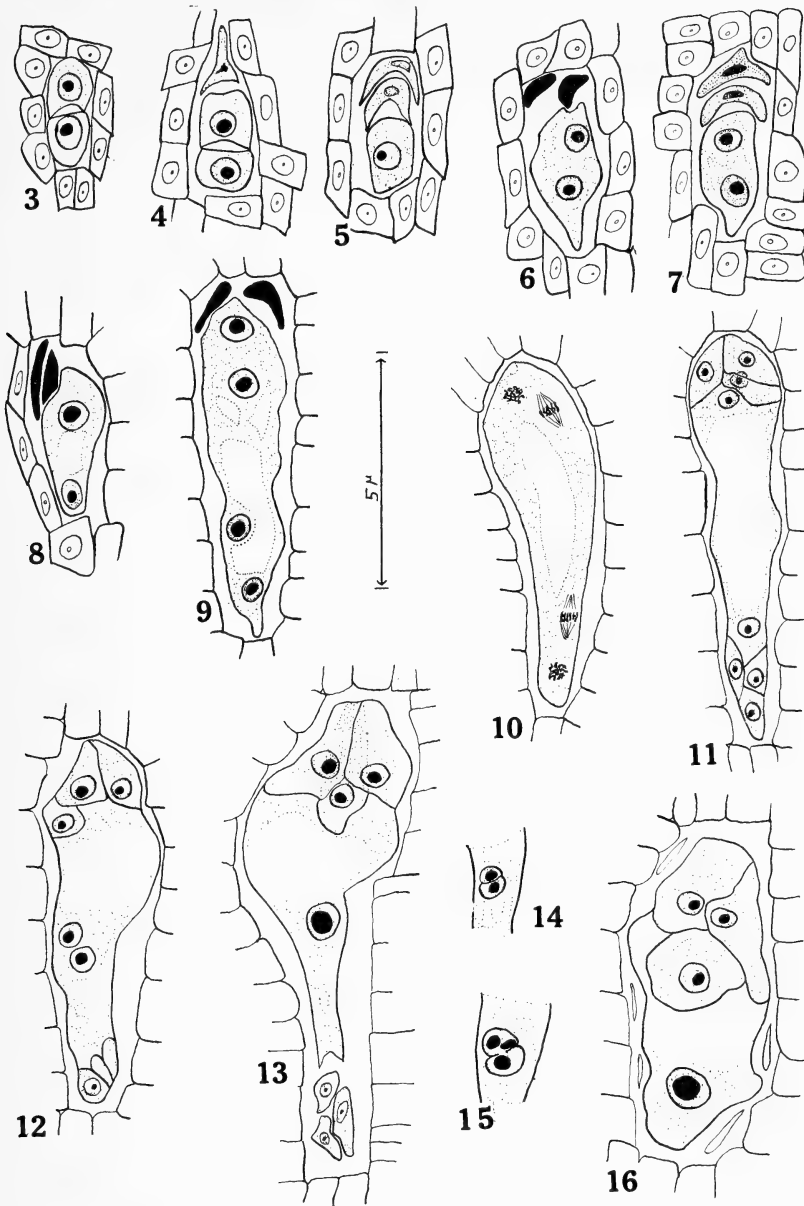
MEGASPOROGENESIS

The ovules are formed in two rows within each locule and develop from its base toward the apex. As many as twelve to eighteen ovules are initiated in each locule although only two to six usually form gametophytes and these are most often located near the base of the locule. The ovules may cease development and become degenerate during any stage of megasporogenesis or megagametogenesis.

The megaspore mother cell is first distinguishable within the young ovule, embedded beneath seven to nine layers of nucellar cells. This cell is large, nearly oval in shape, with dense cytoplasm, and a large vesicular nucleus (fig. 1). Frequently as many as five large cells are present within the nucellus and have the appearance of megaspore mother cells (fig. 2). Only one of these cells in an ovule undergoes the meiotic divisions, and it is then that the functional megaspore mother cell can first be determined. In such ovules the functional mother cell is most often located near the center of the group of enlarged cells. After meiosis I is completed, cytokinesis takes place, and a dyad of cells of approximately the same size, each with dense cytoplasm and a large, deeply staining nucleus containing a prominent nucleolus, is formed (fig. 3). The chalazal dyad cell completes meiosis II and cytokinesis takes place, but the micropylar dyad

FIGS. 3-5. Megasporogenesis. 3, dyad cells formed from meiosis I of megaspore mother cell; 4, micropylar dyad cell disintegrating while chalazal dyad cell undergoes meiosis II and forms two megaspores; 5, enlarging chalazal megaspore with upper megaspore and micropylar dyad cell disintegrating.

FIGS. 6-16. Megagametogenesis. 6, young 2-nucleate megagametophyte; 7, beginning of vacuoles in 2-nucleate megagametophyte; 8, vacuoles have coalesced in center



of 2-nucleate megagametophyte; 9, 4-nucleate megagametophyte; 10, nuclear divisions to form 8-nucleate megagametophyte; 11, egg apparatus formed, also antipodals, but before migration of polar nuclei; 12, polar nuclei have migrated to center of megagametophyte; 13, polar nuclei have fused and antipodals are disintegrating; 14, fusion of two polar nuclei; 15, fusion of two polar nuclei and sperm nucleus; 16, enlarged egg apparatus of mature megagametophyte.

cell degenerates without undergoing this division (fig. 4). The linear triad of cells which results from this activity consists of the degenerating micropylar dyad cell and the two megaspores formed by the chalazal dyad cell (fig. 4). In all cases observed the chalazal megaspore enlarged further and became the only functional megaspore (fig. 5). The other two cells of the triad are soon pushed aside by the developing megagametophyte which presses them against the surrounding nucellar cells where they gradually disintegrate (figs. 5, 6, 7, 8, 9).

MEGAGAMETOGENESIS

In the ovules studied the chalazal megaspore increases in size, the nucleus divides, and gradually a 2-nucleate megagametophyte is formed (fig. 6). As the cell continues to enlarge, two small lateral vacuoles appear in the cytoplasm, one to either side of the nuclei (fig. 7). Growth of the megagametophyte continues and the two lateral vacuoles coalesce into a single large central vacuole as one of the nuclei and part of the cytoplasm move toward the micropylar end and the other nucleus and remainder of the cytoplasm move toward the chalazal end of the cell (fig. 8). Rapid growth of the megagametophyte continues and each of the nuclei undergoes another division forming a 4-nucleate cell with a pair of nuclei at either end oriented along the major axis of the megagametophyte (fig. 9). The four nuclei undergo a division with one spindle at each end of the megagametophyte oriented along the major axis of the cell and one spindle at each end oriented perpendicular to the major axis (fig. 10). This division results in an 8-nucleate megagametophyte with four nuclei located at either end. The megagametophyte elongates further and the egg apparatus, consisting of three cells, is soon formed at the micropylar end of the megagametophyte (fig. 11). There is no discernible differentiation into an egg cell and two synergids at this time. Three distinct, comparatively large, antipodal cells are formed at the chalazal end of the megagametophyte (fig. 11). The two polar nuclei, one located beneath the egg apparatus and the other directly above the antipodal cells, are immersed in thin cytoplasm and separated by a central vacuole. The polar nuclei soon migrate toward the center of the megagametophyte and lie next to each other (fig. 12). The antipodal cells begin to degenerate (fig. 12) and then separate from each other and the primary endosperm cell (fig. 13). At the same time the micropylar end, containing the egg apparatus, increases in size (fig. 13). The egg cell is soon distinguished from the two synergids by its larger nucleus (fig. 16). The polar nuclei may fuse to form a secondary nucleus (fig. 14) or fusion may be delayed until the sperm nucleus enters, in which case all three nuclei fuse at once to form the primary endosperm nucleus (fig. 15). With the disintegration of the antipodal cells the megagametophyte becomes broader, the single secondary nucleus (or the primary endosperm nucleus, as the case may be) and the egg apparatus enlarge (fig. 16). The cytoplasm of the two synergid

cells becomes vacuolated and a small vacuole often appears above the egg nucleus within the greatly enlarged egg cell.

SUMMARY

The megaspore mother cell is embedded beneath seven to nine nucellar cell layers. There are frequently more than one and sometimes as many as five large cells which resemble megaspore mother cells in a single ovule, but only one of these cells functions. A linear triad of cells is formed as the chalazal dyad cell undergoes meiosis II and the micropylar dyad cell does not. In previously studied species of the Hamamelidaceae only one potential megaspore mother cell forms in each ovule and both dyad cells undergo meiosis II to form a linear tetrad of megaspores. The chalazal megaspore develops into the megagametophyte in all species studied. The pattern of development is essentially that of the *Polygonum* type listed by Maheshwari (1950).

Department of Biology
Randolph-Macon Woman's College
Lynchburg, Virginia

LITERATURE CITED

- FLINT, F. F. 1957. Megasporogenesis and megagametogenesis in *Hamamelis virginiana* L. Va. Jour. Sci. 8(3):185-189.
———. 1957A. Megasporogenesis and megagametogenesis in *Fothergilla gardenii* Murr. and *Fothergilla major* Lodd. Trans. Am. Micro. Soc. LXXVI(3):307-311.
JOHANSEN, D. A. 1940. Plant microtechnique. McGraw-Hill, N. Y.
MAHESHWARI, P. 1950. An introduction to the embryology of the angiosperms. McGraw-Hill, N. Y.

REVIEWS

A Flora of San Francisco, California. By JOHN THOMAS HOWELL, PETER H. RAVEN, AND PETER RUBTZOFF. 157 pp., 20 figs., 1 map. The Wasmann Journal of Biology, Vol. 16, No. 1. 1958. Published in book form by the University of San Francisco. Paper. \$3.00.

In spite of the many people now living within the city limits of San Francisco, an amazing number of native plants are still to be found. This is largely due to the hilliness of the city. The hilltops, bluffs, and cliffs provide refuges, many of which have not as yet been commercially exploited. Some habitats, notably the marshes and sand dunes, are rapidly disappearing. On Bernal Heights, however, *Dodecatheon patulum* var. *bernalinum* still grows at its type locality and *Aristolochia californica* is still to be found in ravines near Lake Merced.

In 1892, Katharine Brandegee listed 605 taxa of vascular plants in her "Catalogue of the Flowering Plants and Ferns Growing Spontaneously in the City of San Francisco." Howell, Raven, and Rubtzoff list 1132 species, subspecies, varieties, forms, and hybrids as growing spontaneously in San Francisco now or in the past. Of these, about 42 per cent are introduced plants and about 19 per cent have not been collected since 1940 and are probably now extinct locally. A number of garden escapes are included. Among them are: *Pseudosasa japonica*, *Pittosporum crassifolium*, 2 species of *Cotoneaster*, 3 species of *Acacia*, *Albizia lophantha*, *Cassia tomentosa*, *Ruta chalepensis*, and *Buddleia davidii*. The main criterion used for inclusion of a particular garden escape is "whether or not the plant could survive in San Francisco without

the aid of summer irrigation." Ample attention also has been paid to weeds. The senior author in particular has collected in disturbed areas in San Francisco, along railroad tracks and in the vicinity of stockyards, and has found such weeds as *Kochia scoparia*, a plant not previously reported from central California. The introduction to the flora contains a short discussion of the vegetation and the geology of San Francisco and a short history of past botanical work on the flora of San Francisco. Descriptions and keys are not provided, but detailed distributional notes are included, and specimens are cited for most species. Authors' names are spelled out in full. The photographs, most of them original, picture typical plant communities, and some of them show the inroads which *civilization* is making into the environment.

This work is a most welcome addition to the existing local floras of various parts of the San Francisco Bay region and will be especially useful to those interested in the distribution and future migration of weeds and garden escapes. It may be obtained at the University of San Francisco Bookstore, San Francisco.—JOHN H. THOMAS, Dudley Herbarium, Stanford University.

Die Nadelgehölze. By GERD KRÜSSMANN. 304 pp., 362 figs. Paul Parey, Berlin and Hamburg, 1955. D.M. 39.60.

The author of "Die Laubgehölze" (Broadleaved Trees) by the same publisher has now made a contribution to the literature on gymnosperms. The term "Nadelgehölze" (Needle-leaved Trees) is used by the author as a traditional convenient term for all gymnosperms, including broad-leaved ones such as *Ginkgo biloba*, *Agathis* and *Podocarpus*.

Gerd Krüssmann, dendrologist of the Botanical Garden in Dortmund, Germany, is the General Secretary of the International Dendrology Union. A revised edition of Beissner-Fitschen's "Handbuch der Nadelholzkunde" (Handbook of Gymnosperms) was expected after its third edition which was published in 1930. Although the present book does not represent a revision of this well-known "Handbook of Gymnosperms," it answers a great need in dendrology.

Krüssman's book not only emphasizes the gymnosperms hardy in Central Europe, but it also attempts to cover very many other species, varieties and forms that are not hardy in Central Europe. The book is illustrated with excellent line drawings and black and white photographs. The source of each illustration is cited carefully by the author.

The introductory chapter gives a good popular account on the gross morphology of gymnosperms and explains the botanical terminology used for the descriptions throughout the text. This certainly increases the practical value of the book among gardeners, beginners and amateurs. However, some may expect a more proper and careful usage of such terms as "flower" and "fruit" which are generally applied only to angiosperms. The author points out the absence of perianth and ovaries among gymnosperms, but he nevertheless uses these terms freely in the text. "Male" microsporangiate and "female" (ovulate or megasporangiate) cones (strobili) would be the proper terms to apply to the reproductive structures of gymnosperms. Three types of strobili are distinguished under the heading of "Fruits and seeds": 1) Zapfen (cones), 2) Beerenzapfen (berry-like cones), 3) Früchte (fruits). Indeed it is pleasing to note the proper application of the term "berry-like cones" to designate the ovulate cones of *Juniperus* instead of the term "berries" which is a common mistake repeated in various manuals. On the other hand, the term "Früchte" (fruits) is used improperly to designate the fleshy seeds of *Cephalotaxus*, *Torreya*, *Taxus*, *Podocarpus* and *Ginkgo*. A fruit is a matured ovary of an angiosperm, and the usage of the term should be restricted to angiosperms.

The systematic arrangement follows the classification scheme proposed by Professor R. Florin, Stockholm. According to this scheme the Gymnospermae is divided into four classes: Class 1, Cycadopsida, comprises the orders Pteridospermae, Caytoniales, Cycadales, Nilssoniales, Bennettiales, Pentoxylales, Ginkgoales; Class 2,

Coniferopsida, covers Cordaitales and Coniferae; Class 3, Taxopsida, includes only one order, Taxales; Class 4, Chlamydospermae, includes one order, Gnetales.

It is interesting to note that this system of classification segregates *Podocarpus*, *Cephalotaxus* and their allies from the Taxaceae and treats them as separate families such as Podocarpaceae and Cephalotaxaceae under the order Coniferae. The Taxaceae comprises the genera *Amentotaxus*, *Torreya*, *Austrotaxus*, *Nothotaxus* and *Taxus*.

The book gives the descriptions of the orders, families and genera of recent gymnosperms, which are summarized nicely without unnecessary details. The lack of keys seems to be a disadvantage which would render the use of the book somewhat difficult among beginners and amateurs. However, this disadvantage is highly reduced by the comparison of specific differences under each genus, these being presented in beautifully prepared tabular form.

The special part of the book dealing with the descriptions of the genera and species of gymnosperms covers 261 pages in which the genera as well as the species of each genus are arranged alphabetically. The generic descriptions cover gross morphological features of the vegetative and reproductive structures, but also provide some limited information at the anatomical level such as the number and position of resin ducts, vascular bundles, stomatal bands, pollen grains, basic chromosome numbers, etc.

The approximate number of species under each genus is cited in all cases, but I believe some of these figures represent out-of-date information. For instance the approximate number of the species of the genus *Pinus* is cited as "80 species," which agrees with the citation of Engler and Gilg's "Syllabus der Pflanzenfamilien" (cf. 3rd edition, 1919). Most recent publications accept 90 or more species under this genus. Likewise 40 species are cited for *Juniperus* while other recent publications cite as many as 70 species for this genus. Naturally all newly established species are subject to acceptance or rejection by taxonomists, but I believe that the remarkable increase in the number of species of gymnosperms in recent years is the result of more careful and detailed studies. Therefore this increase is to be expected and should be taken into consideration.

The distribution maps of genera are quite practical and more or less of the same nature as the distribution maps of the genera and families presented in J. Hutchinson's "Families of Flowering Plants." Ranges of distribution and places of main occurrences are also given following the descriptions of genera and species. In some instances the distribution maps disagree with cited ranges and sometimes incomplete data are also obvious. For example the distribution map of the European species of *Abies* taken after Mattfeld is somewhat different from Krüssman's distribution map of this genus. The latter's figure 4 excludes the distribution of *Abies nordmanniana* and fails to indicate the western extension of *A. alba* in Pyrenees. Likewise the distribution of *Torreya californica* is neglected in figure 37 although it is cited under the description of this species on page 285.

Consistent spelling of the locality names would be desirable. "Cilicischen Taurus" appears intermittently with the germanized spelling, "Zilizischen Taurus." Furthermore the usage of ancient, discontinued names of localities should be avoided wherever possible. For example, "Cilicia" of ancient ages has now been replaced by the Turkish name, "Adana."

Rather a large number of gymnosperms of the Pacific Coast of the United States and Canada is included in the book, and therefore it can serve as a good reference to the botanists, students and amateurs of this area. All species of the genus *Abies* along the Pacific Coast are included in the work. With the exception of *Cupressus pygmaea* Sarg. and *C. sargentii* Jepson, all other *Cupressus* species native to the Pacific Coast are taken into account. Furthermore the book comprises all Pacific Coast pines except two recently described species, *Pinus remorata* Mason (1930) and *P. washoensis* Mason et Stockwell (1945). Three-needle pines such as *Pinus attenuata*, *P. coulteri* and *P. jeffreyi* are listed under the two-needle pines on page 209 erroneously although the cross sectional outlines of their needles on the following page show clearly that they belong to the three-needle section of the genus.

Sequoia sempervirens (Lamb.) Endl. and *Sequoiadendron giganteum* (Lindl.) Buchholz are treated under the same genus although the proposal of J. T. Buchholz regarding the generic segregation of the sequoias is accepted by many in modern literature. The reviewer believes that there are more than sufficient morphological, geographic and ecological differences between the two sequoias to justify their segregation.

The book contains very valuable information on the horticultural uses of different varieties and garden forms of gymnosperms. Those who can correlate the hardiness to conditions of Central Europe with the hardiness to conditions of other geographic areas can make a good use of the knowledge given in the book for judging the suitability of various gymnosperms.

Toward the end of the book a small chapter enumerates the most important pineta in the world. Seventy-seven institutions or localities are listed for eighteen countries in Europe and North America. The author admits the incompleteness of his list and expresses his desire for receiving the recommendations of his readers for the extension of the list. In this connection I would like to suggest the addition of the following arboreta in the United States: Eddy Arboretum at the Institute of Forest Genetics in Placerville, California, which has the most complete living collection of *Pinus* in the world; Westtown School Arboretum in Philadelphia for *Abies* and *Picea*; Morton Arboretum in Lisle, Illinois, for *Picea*, *Taxus* and *Juniperus*.

The list of literature is short, but it comprises the principal standard references on gymnosperms.

Finally, an index of invalid synonyms of gymnosperms concludes the book. This index is extremely useful to the reader since it clears many confusions in nomenclature.

In general the book is a treasury of information about gymnosperms in spite of its relatively small size. Both the author as well as the publisher deserve congratulations for this valuable publication.—BAKİ KASAPLIGİL, Department of Biology, Mills College, Oakland 13, California.

NOTES AND NEWS

The second issue of the Index to Plant Chromosome Numbers, compiled from nearly 300 journals published in 1957, is now ready for distribution. There are around 2000 listings of original chromosome counts from the entire plant kingdom and a bibliography of 196 papers from which the listings were taken. Preparation of the Index has been supported in part by a grant from the National Science Foundation of the U.S.A. The price of each issue is \$1. Orders for subscriptions may be sent to:

Dr. C. Ritchie Bell
Department of Botany
University of North Carolina
Chapel Hill, North Carolina, U.S.A.

Information on the location and history of any trees of *Cedrus* or *Sequoia* (including *Sequoiadendron*) which were planted in the Pacific coastal states prior to 1900 will be appreciated by E. E. Stanford, Department of Botany, College of the Pacific, Stockton, California.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$15 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*, Part 1. *The Herbaria of the World*. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$4.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany
University of California, Berkeley 4, California



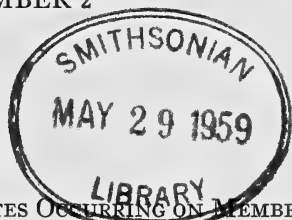
MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 2

APRIL, 1959

Contents



	PAGE
RED ALGAL PARASITES OCCURRING ON MEMBERS OF THE GELIDIALES, <i>Kung-Chu Fan</i> and <i>George F. Papenfuss</i>	33
XEROPHYLLUM TENAX, SQUAWGRASS, ITS GEOGRAPHIC DISTRIBUTION AND ITS BEHAVIOUR ON MOUNT RAIN- IER, WASHINGTON, <i>Sue Merrick Maule</i>	39
DOCUMENTED CHROMOSOME NUMBERS OF PLANTS	49
TYPIFICATION OF PROSOPIS ODORATA TORR. & FREM. (LEGUMINOSAE), <i>Lyman Benson</i>	53
TWO NEW SPECIES OF HELIANTHUS FROM NEW MEXICO, <i>R. C. Jackson</i>	54
CHROMOSOME COUNTS IN THE SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). III, <i>Barid B. Mukherjee</i> and <i>R. K. Vickery, Jr.</i>	57
REVIEW: G. Erdtman, <i>Pollen and Spore Morphology/ Plant Taxonomy</i> (<i>Jane Gray</i>)	62
NOTES AND NEWS: THE OCCURRENCE OF PILOSTYLES THURBERI (RAFFLESIAEAE) IN CALIFORNIA, <i>Job Kuijt</i> ; NOTES ON THE FLORA OF ARIZONA, <i>Charles T. Mason, Jr.</i>	63

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—WINSLOW R. BRIGGS.

Department of Biology, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: James R. Sweeney, San Francisco State College, San Francisco, California. First Vice-president: Baki Kasapligil, Mills College, Oakland, California. Second Vice-president: Henry J. Thompson, Department of Botany, University of California, Los Angeles, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: Winslow R. Briggs, Department of Biology, Stanford University, Stanford, California.

RED ALGAL PARASITES OCCURRING ON MEMBERS OF THE GELIDIALES

KUNG-CHU FAN AND GEORGE F. PAPENFUSS¹

Three genera and four species of red algae have been reported as parasitic on the various members of the Gelidiales. They are *Syringocolax macroblepharis* Reinsch (1875; Martin and Pocock, 1953), *Gelidiocolax microsphaerica* Gardner (1927), *Choreocolax suhriae* Martin et Pocock (1953), and *C. margaritoides* Martin et Pocock (1953). These species are reviewed and two parasitic red algae occurring on *Pterocladia*, also a member of the Gelidiales, collected by Setchell in New Zealand in 1904 and by Papenfuss in New Zealand in 1949 and in Hawaii in 1942, are described as new.

Gelidiocolax microsphaerica was obtained in 1911 by Gardner on *Gelidium pulchrum* growing at Balboa Beach, Orange County, California. Dangeard in 1952 reported *Gelidiocolax microsphaerica* (in error as *G. hemisphaerica*) from Dakar. Subsequently, the species was reported by Dawson (1952, 1953) from the shores of Isla San Martín, Baja California. Careful examination of specimens of *Gelidium pulchrum* (collected at Punta Descanso, Baja California, Mexico, Dawson 131-45, April 8, 1945, UC 694021) has resulted in the finding of additional specimens of *Gelidiocolax microsphaerica*. The tubercle produced by this species is spherical in form, about 175-225 μ in diameter, and difficult to detect without the aid of a hand lens; it is mostly composed of the reproductive tissue of the parasite. The carpogonial branch is composed of two cells, the spermatangia are produced in chains, and the tetrasporangium is cruciately divided. Although currently placed in the Gelidiaceae (cf. J. & G. Feldman 1958), it appears more likely that *Gelidiocolax* belongs in the Choreocolacaceae.

Choreocolax suhriae is parasitic on *Suhria vittata* in South Africa; the wart-like swelling is composed of a dense mixture of parasite and host tissues; it is about 2-3 mm. broad and about 1 mm. high when mature. During maturation, many or sometimes most of the surface cells of the parasite produce reproductive organs. Its carpogonial branch is two-celled like that of *Gelidiocolax microsphaerica* and not four-celled as in *Choreocolax polysiphoniae*, which is the type species of *Choreocolax* (Sturch 1926). In fact *C. suhriae* resembles *G. microsphaerica* so much that it should be placed in *Gelidiocolax* instead of in *Choreocolax*. The following combination is therefore proposed: ***Gelidiocolax suhriae*** (Martin et Pocock) Fan et Papenfuss, comb. nov. (*Choreocolax suhriae* Martin et Pocock 1953, p. 48).

Choreocolax margaritoides is parasitic on *Beckerella pinnatifida* in

¹ This study was aided by a grant-in-aid from the National Science Foundation to the second author. Dr. Mary A. Pocock kindly furnished the material of *Choreocolax suhriae* and *C. margaritoides*.

South Africa. Tetrasporic specimens of this species were examined. The pustule is roundish, 200–290 μ in diameter, and is mostly composed of parasite tissue. This species is closely related to *Gelidiocolax microsphaerica*. However, the tetrasporic pustule is slightly larger than that of *G. microsphaerica*, which is 175–225 μ in diameter. The tetraspores of *C. margaritoides* are 12–18 μ in length; those of *G. microsphaerica* are 22–28 μ in length. In our opinion *C. margaritoides* is a species of *Gelidiocolax*. The following combination is therefore proposed: ***Gelidiocolax margaritoides*** (Martin et Pocock) Fan et Papenfuss, comb. nov. (*Choreocolax margaritoides* Martin et Pocock 1953, p. 50).

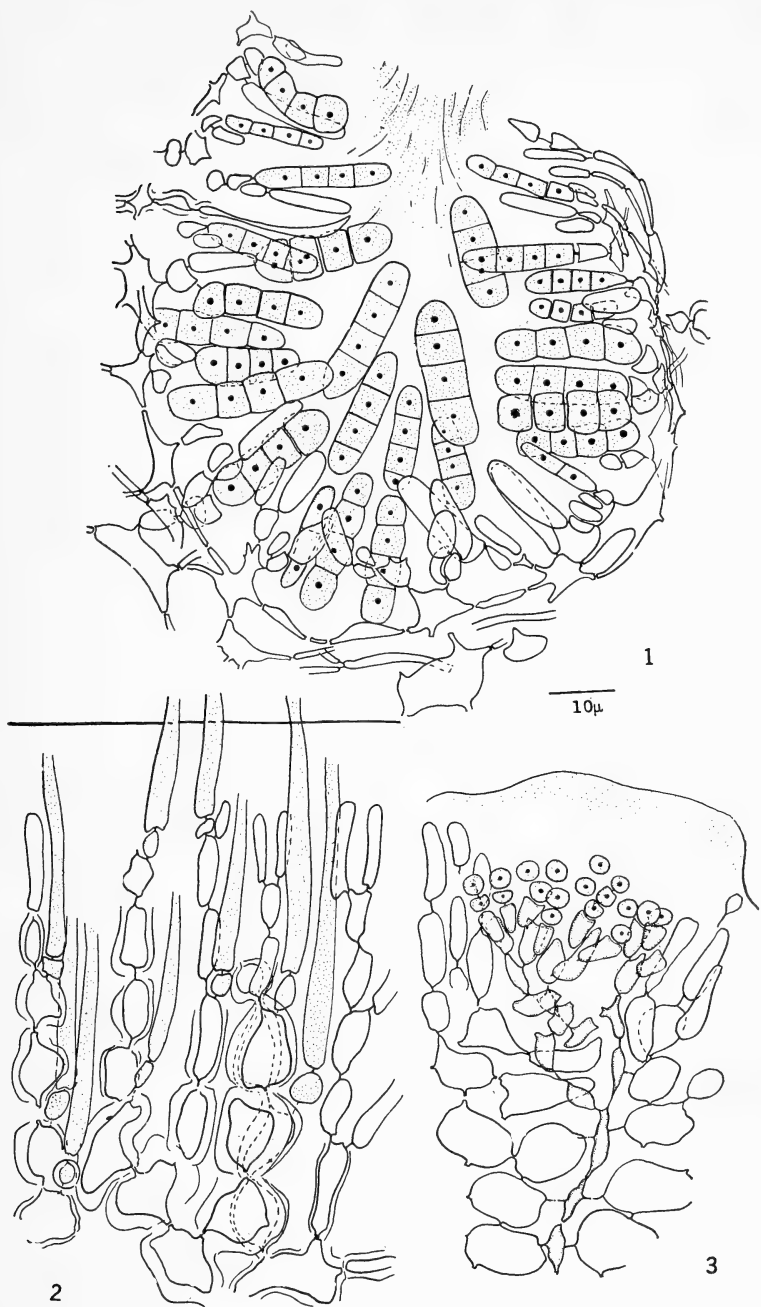
Gelidiocolax mammillata Fan et Papenfuss sp. nov. Planta in *Pterocladia* sp. parasitica, constans e filamentis multis irregulariter ramosis, in telam hospitis profunde penetrantibus, tuberculum solidum verruciforme efficientibus; tuberculum maturum 0.3–1 mm. lat., 0.3–0.5 mm. alt., e tela et hospitis et parasitici compositum, proiectiones mammillatas multas in superficie habens; cystocarpi, spermatangia, tetrasporangiaque in proiectionibus mammillatis praecipue producta, et in cubiculis per telas hospitis effectis reperta; ramus carpogonialis bicellularis; spermatangia in catenis formata, per septa transversa ab extremitatibus terminalibus cellularum-matrum spermatangialium successive abscissa; tetrasporangia cruciate divisa.

Plant parasitic on *Pterocladia* sp., consisting of many irregularly branched filaments which penetrate deeply into the host tissue, producing a wart-like solid tubercle; tubercle when mature 0.3–1 mm. wide and 0.3–0.5 mm. high, composed of both host and parasite tissues, with many mammillate projections on the surface; cystocarps, spermatangia and tetrasporangia produced primarily in the mammillate projections and occurring in chambers produced by host tissue; carpogonial branch two-celled; spermatangia formed in chains, successively cut off by transverse septa from the terminal ends of the spermatangial mother cells; tetrasporangia cruciately divided.

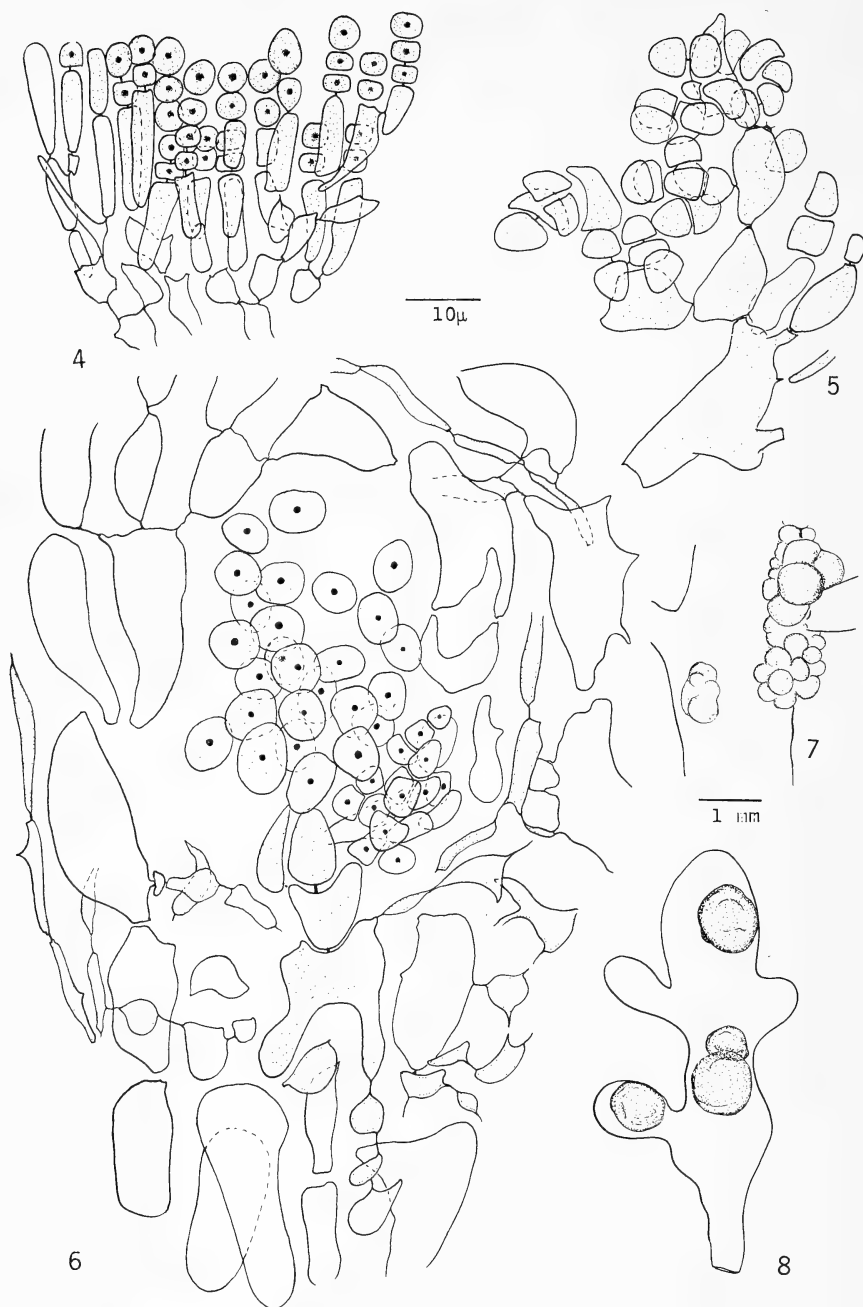
Type. Hanauma Bay, Oahu, Hawaiian Islands, March 1, 1942. *G. F. Papenfuss* (UC 1058497). Figs. 3, 6, 7, 9, 10.

Pterocladiophila hemisphaerica Fan et Papenfuss gen. et sp. nov. Planta in *Pterocladia lucida* parasitica, constans e filamentis multis irregulariter ramosis in telam hospitis profunde penetrantibus, tuberculum solidum plus minusve hemisphericum efficientibus; tuberculum maturum 0.4–1 mm. lat., 0.4–0.8 mm. alt. e telis et hospitis et parasitici compositum, in superficie inaequale; cystocarpi, spermatangia, tetrasporangiaque in concepticulis formata; ramus carpogonialis bicellularis; spermatangia in catenis producta, per septa transversa ab extremitatibus terminalibus cellularum-matrum spermatangialium successive abscissa; tetrasporangia zonate divisa, pavimento lateribusque conceptaculi introrsum obducentia.

Plant parasitic on *Pterocladia lucida*, consisting of many irregularly branched filaments which penetrate deeply into the host tissue, producing



FIGS. 1, 2. *Pterocladophila hemisphaerica*: 1, tetrasporangia within the conceptacle; 2, carpogonial branches. FIG. 3. *Gelidiocolax mammillata* (marginal stippling) with spermatangia (solid stippling).



FIGS. 4, 5, 8. *Pterocladophila hemisphaerica*: 4, spermatangia; 5, part of gonimoblast and carposporangia; 8, habit of parasite on *Pterocladia lucida*. FIGS. 6, 7. *Gelidiocolax mammillata* (stippled cells): 6, gonimoblast with carpösporangia; 7, habit of parasite on *Pterocladia* sp.



FIGS. 9, 10. *Gelidiocolax mammillata* (marginal and solid stippling); 9, tetrasporangia; 10, carpogonial branches.

a more or less hemispherical solid tubercle; tubercle when mature 0.4–1 mm. wide and 0.4–0.8 mm. high, composed of both host and parasite tissues, uneven on surface; cystocarps, spermatangia and tetrasporangia formed in conceptacles; carpogonial branch two-celled; spermatangia produced in chains, successively cut off by transverse septa from the terminal ends of the spermatangial mother cells; tetrasporangia zonately divided, lining floor and sides of the conceptacle.

Type. Island Bay near Wellington, New Zealand, June 1904. *W. A. Setchell* 6098 (UC 1141475) [separated from host plant, *Pterocladia lucida* (UC 95977)]. Figs. 1, 2, 4, 5, 8.

Additional material. New Zealand: Kaikoura, 17 February 1949, *Moore* and *Papenfuss* (UC 1058496); Goose Bay 10 miles south of Kaikoura, 18 February 1949, *Moore* and *Papenfuss* (UC 1058495).

Pterocladophila is readily distinguished by its zonately divided tetrasporangia (fig. 1), formed within conceptacles, from all the known genera of parasitic red algae except *Chaetolithon* Foslie (1898; Kylin 1956), *Choreonema* Schmitz (1889; Suneson 1937), and *Polyporolithon* Mason (1953) in which three genera the sporangia are also zonately divided and localized in conceptacles. *Chaetolithon*, *Choreonema* and *Polyporolithon* belong to the family Corallinaceae, which family is almost exclusively composed of calcareous algae. Also, as far as known, the spermatangia are not produced in chains in the Corallinaceae as they are in *Pterocladophila*.

Pterocladophila cannot be assigned to the Choreocolacaceae owing to its zonately divided tetrasporangia which are formed in deeply sunken conceptacles (fig. 1). Nor can it be assigned to the Corallinaceae (although it resembles some members of this family by its simple, two-celled carpo-

gonial branch and its zonately-divided tetrasporangia produced in conceptacles) because it is not calcified as all the Corallinaceae are with the exception of *Schmitziella* (Batters 1892, Suneson 1944); it also differs from members of this family in having the spermatangia produced in chains (fig. 4). A new family *Pterocladiophilaceae* is therefore suggested here, and this family is tentatively assigned to the order Cryptonemiales. This family is characterized by the following features.

Pterocladiophilaceae Fan et Papenfuss fam. nov. Thallus haud calcifactus ramo carpogonio bicellulato spermatangia catenulata septis transversis termino cellulae maternae spermatangialis enata tetrasporangia zonatim divisa in conceptaculis circumscripta.

Thallus not calcified; carpogonial branch two-celled; spermatangia produced in chains, successively cut off by transverse septa at the terminal end of the spermatangial mother cell; tetrasporangia zonately divided, formed in conceptacles.

Department of Botany,
University of California,
Berkeley, California

LITERATURE CITED

- BATTERS, E. A. L. 1892. On *Schmitziella*; a new genus of endophytic algae, belonging to order Corallinaceae. *Ann. Bot.* 6:185-194, pl. 10.
- DANGEARD, P. 1952. Algues de la presqu'île du Cap-Vert (Dakar) et de ses environs. *Botaniste* 36:195-329, 15 figs., pls. 14-21.
- DAWSON, E. Y. 1952 [1953]. Marine red algae of Pacific Mexico. Part I. Bangiales to Corallinaceae subf. Corallinoideae. *Allan Hancock Pac. Exped.* 17:1-239, pls. 1-33.
- . 1953. [1954]. Notes on Pacific Coast marine algae. VI. *Wasmann Jour. Biol.* 11:323-351, pls. 1-6.
- FELDMANN, J. and GENEVIÈVE FELDMANN. 1958. Recherches sur quelques Floridees parasites. *Revue Gen. Bot.* 65:49-127, figs. 1-30, pls. 1-2.
- FOSLIE, M. 1898. List of species of the Lithothamnina. *K. Norske Vidensk. Selsk. Skr.* 1898(3). 11 pp.
- GARDNER, N. L. 1927. New Rhodophyceae from the Pacific coast of North America. III. *Univ. Calif. Publ. Bot.* 13:333-369, pls. 59-71.
- KYLIN, H. 1956. Die Gattungen der Rhodophyceen. xv+673 pp., 458 figs. Lund.
- MARTIN, MARGARET T. and MARY A. POCKOCK. 1953. South African parasitic Florideae and their hosts. 2. Some South African parasitic Florideae. *Jour. Linn. Soc. London Bot.* 55:48-64, figs. 1-7, pls. 10-12.
- MASON, LUCILE R. 1953. The crutaceous coralline algae of the Pacific coast of the United States, Canada, and Alaska. *Univ. Calif. Publ. Bot.* 26:313-390, pls. 27-46.
- REINSCH, P. F. 1875. Contributions ad algologiam et fungologiam. xii+104 pp., 130 pls. Norimbergae.
- STURCH, H. H. 1926. *Choreocolax polysiphoniae*, Reinsch. *Ann. Bot.* 40:585-605, figs. 1-15.
- SUNESON, S. 1937. Studien über die Entwicklungsgeschichte der Corallinaceen. *Lunds Univ. Årsskr. N. F. Avd. 2*, 33(2). 102 pp., figs. 1-42, pls. 1-4.
- . 1944. Notes on *Schmitziella* endophloea. *K. Fysiogr. Sällskap. Lund Förhandl.* 14:239-245, figs. 1-2.
- SCHMITZ, F. 1889. Systematische Übersicht der bisher bekannten Gattungen der Florideen. *Flora* 72:435-456, pl. 21.

XEROPHYLLUM TENAX, SQUAWGRASS, ITS GEOGRAPHIC
DISTRIBUTION AND ITS BEHAVIOUR ON
MOUNT RAINIER, WASHINGTON¹

SUE MERRICK MAULE²

The objectives of the present study of *Xerophyllum tenax* are twofold; to compile information regarding its geographic distribution and to study the specific environmental requirements necessary for its vegetative growth and blossoming on Mount Rainier, Washington. Since the field observations have been confined to a single season, the results presented must be considered as tentative. In order to study the environmental requirements fully, stations with permanent protected plots would have to be established throughout the range of the species and observations made over a period of years.

Xerophyllum tenax (Pursh) Nutt. (fig. 1) is a tufted, herbaceous, graminoid, perennial hemicryptophyte having a tuber-like woody root-stock bearing cord-like roots. It bears numerous grass-like, keeled, rigid leaves 5–10 dm. long, 5–10 mm. wide at the base and gradually tapering to a narrow, stiff and wiry tip, the margins rigid and serrulate (Peck, 1941; Jepson, 1951). According to Dr. D. B. Lawrence (personal communication), the young seedlings can be distinguished from those of *Carex* species by a grey-white bloom which covers the leaves of the *Xerophyllum*. Flowering occurs between May and September. The inflorescence stalks, 3–15 dm. high, are covered by leaf-like bracts which are reduced toward the top, and the raceme, 1–2 dm. long, is very dense, with slender pedicels 2–5 cm. long. The perianth is cream-colored, with lanceolate segments 6–10 mm. long, the stamens surpass the perianth, and the capsule is broadly ovoid, acute, 5–7 mm. long.

Xerophyllum tenax is found from west-central California northward to northwestern Washington, and from Yellowstone National Park northwestward to southwestern Alberta and southeastern British Columbia. Along the coast, at least in northwestern Washington where habitat conditions are specifically recorded, it is found at sea level on bogs, and in the rain-shadow of the Olympic Mountains on gravelly "prairies" (Jones, 1936). It occurs again high in the coast ranges, and from approximately 2000 feet to 7000 feet in the Sierra-Cascade and Rocky Mountain ranges. Thus it is widely separated geographically from the eastern North American species, *X. asphodeloides* (L.) Nutt., which grows at low altitudes on sandy acid pineland of the Atlantic Coastal Plain from North Carolina

¹ Requests for reprints should be addressed to Prof. D. B. Lawrence, Department of Botany, University of Minnesota, Minneapolis 14.

² Sincere thanks to the following, without whose help this contribution would not have been possible: Robert William Maule, for his indispensable work in the field; Dr. Donald B. Lawrence, for help in planning and in organization of results; Dr. Gerald Ownbey, for help with taxonomic problems.



FIG. 1. *Xerophyllum tenax* with an abnormal stunted inflorescence, beside trail, Station 2, Mount Rainier. Normal inflorescence from another plant held in hand.

to New Jersey, and again in the Blue Ridge Mountains and Appalachian Plateau in acid woods of Georgia, North Carolina, Tennessee, and Virginia (Fernald, 1950; Small, 1933).

The geographic distribution of *Xerophyllum tenax* is shown in a map (fig. 2), data for which was compiled from information supplied by staff members of various herbaria (Univ. Calif., Univ. Idaho, Univ. Oreg., Oreg. St. Coll., Univ. Wash., Wash. St. Coll., Nat. Mus. Canada, Univ. Alberta, Univ. Brit. Col.). The species occurs very sparingly in the coastal region near sea level from west-central California to northwestern Washington, and again just below the summits of the coast mountains over almost the same latitudinal range. In the Sierra-Cascade range, it is found from Placer County, California, northward 700 miles to Stampede Pass, Washington, ranging in altitude from approximately 2000 to 6000 feet. It is not known to occur on Mount Shasta. In the Rocky Mountains complex it occurs from 2000 to 7000 feet, with the southernmost limit of its range along the southern boundary of Yellowstone National Park, whence it extends northwestward about 450 miles to Crow's Nest Pass on the British Columbia-Alberta boundary. Westward it extends from the Rocky Mountain divide approximately 200 miles to northern Idaho, reaching its western limit on the summit of Mount Spokane, Washington, at 5800 feet. In Idaho it ranges from southern Lemhi and Valley counties northward to the International Boundary and on in British Columbia to Kootenay Lake, a northwestward extent of 380 miles.

Judging from the differences in habitat that have been reported in the literature, and the broadness of the geographic distribution pattern, it would be reasonable to expect that several races exist within the species. There appear to be definite distributional gaps between the plants growing at sea level along the immediate coastal strip and those growing high in the coast range; similarly a distributional gap exists between the coast ranges and Sierra-Cascades, and another large one between the latter and the Rocky Mountains complex. Although the distribution map (fig. 2) would suggest continuity within the groups running north and south, it is quite possible that the plants growing in the north belong to quite different races from those growing in the outposts along the California coast, the southern Sierras, and the Rocky Mountains in northern Wyoming. It would be very interesting to take individuals from widely different geographical areas and grow them adjacent to each other in experimental plots at several places within the distribution range. Dissimilarities would almost certainly be found.

XEROPHYLLUM TENAX ON MOUNT RAINIER

Between July 13 and August 23, 1955, field work was carried on at Mount Rainier National Park, Washington, and thirty-four stations were established where the species was studied. Figure 3 and Table 1 present the data for these stations and show through description and symbol those characteristics of the plants and of their local environments which were

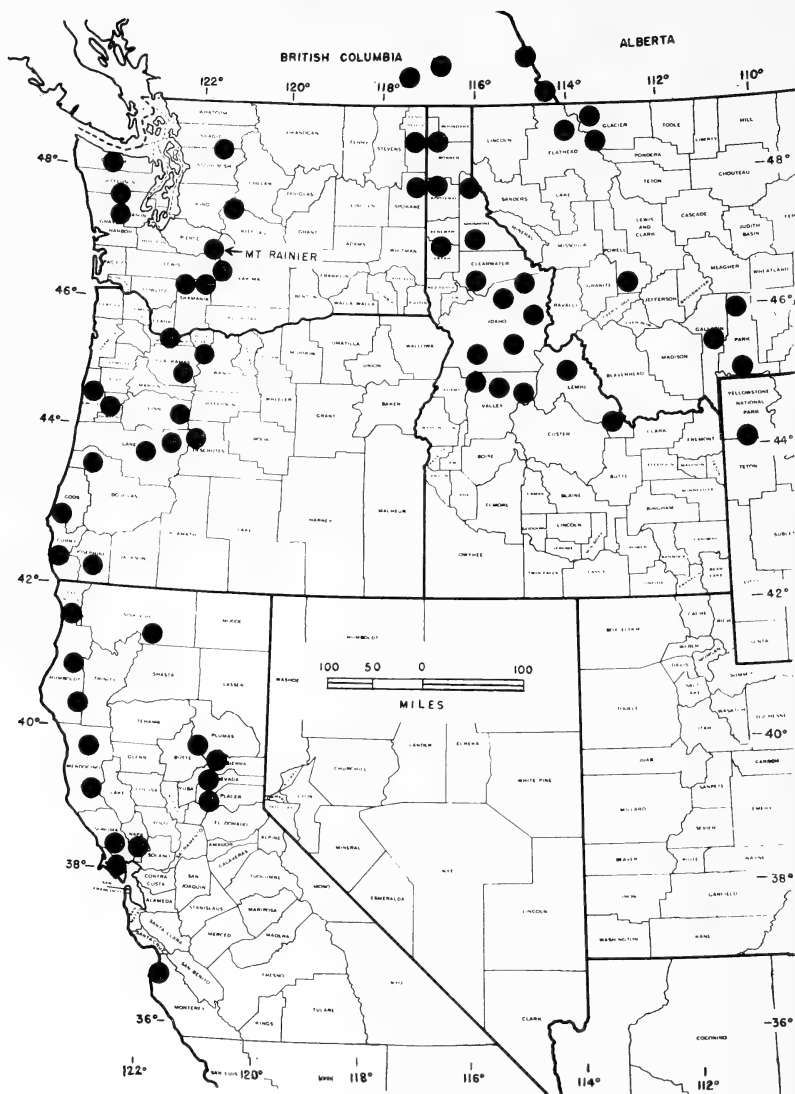


FIG. 2. Distribution map of *Xerophyllum tenax*.

considered significant in determining causes of local distribution. At thirty-three field stations detailed data were recorded as follows: date, time of day, location, elevation, degree and direction of slope, density of spacing measured as minimum distance between *Xerophyllum* clumps, presence of new or old flower stalks, composition of the adjacent vegetation, and history of fire. Where flowering was in progress the following were also recorded: root temperatures in degrees centigrade of flowering and of non-flowering plants three inches below ground surface, height in centimeters of the flower stalk up to base of the raceme, and diameter of flowering stalk in millimeters measured just above basal leaves.

From the data accumulated at these field stations, it appears that the distribution of *X. tenax* within Mount Rainier National Park seems to be influenced by a number of factors, including soil temperature, elevation, and direction and angle of slope.

There are some factors, for example soil water content, which seem to have no apparent influence on its distribution. Individuals were found thriving equally well on dry sunny hillsides and on moisture saturated soil immediately below rapidly disappearing snow banks. This latter observation seems related to the occurrence of *X. tenax* on bogs near sea level. The amount of shading by an overstory also does not seem to be a limiting factor for vegetative growth. Although all the plants found blooming in 1955 were growing in open meadows, light woods, or shrubby areas, and not in dense forests, the ability of the adult plants to survive did not seem to be affected by the amount of shading they received. Plants were found growing well vegetatively in dense forests where little or no direct sunlight filtered through the canopy and also on slopes exposed to the sun for as long as twelve hours a day.

Most of the stations were visited between 10 A.M. and 3:30 P.M. on days of roughly equivalent fair meteorological conditions over a period of about forty days between July 13 and August 25. Recorded air temperatures ranged from 13°C. to 30°C., and soil temperatures three inches below the surface beneath the leaf crowns of *X. tenax* ranged from 9°–18°C.

Within the Park, only the upper limit of distribution could be ascertained, as plants were found growing at the lowest easily accessible boundaries of the Park at 2000 feet and also somewhat lower outside. Although most of the plants were found below 6000 feet, one group of plants was found near Panhandle Gap, Station 22, at 6800 feet. This elevation was the upper limit of all vascular plant growth here, with only lichens and mosses occurring higher. Within this area there were numerous perennial snow fields.

The chief factor that did appear to affect the distribution was direction of slope, and this in turn influences length of snow-free growing season and soil temperature. *Xerophyllum tenax* was found growing on south-facing slopes, one as steep as 55 degrees, at ten stations, on southeast slopes at seven, on southwest slopes at four, on west slopes at three, on east slopes at two, and on north slopes at only one station. In this last

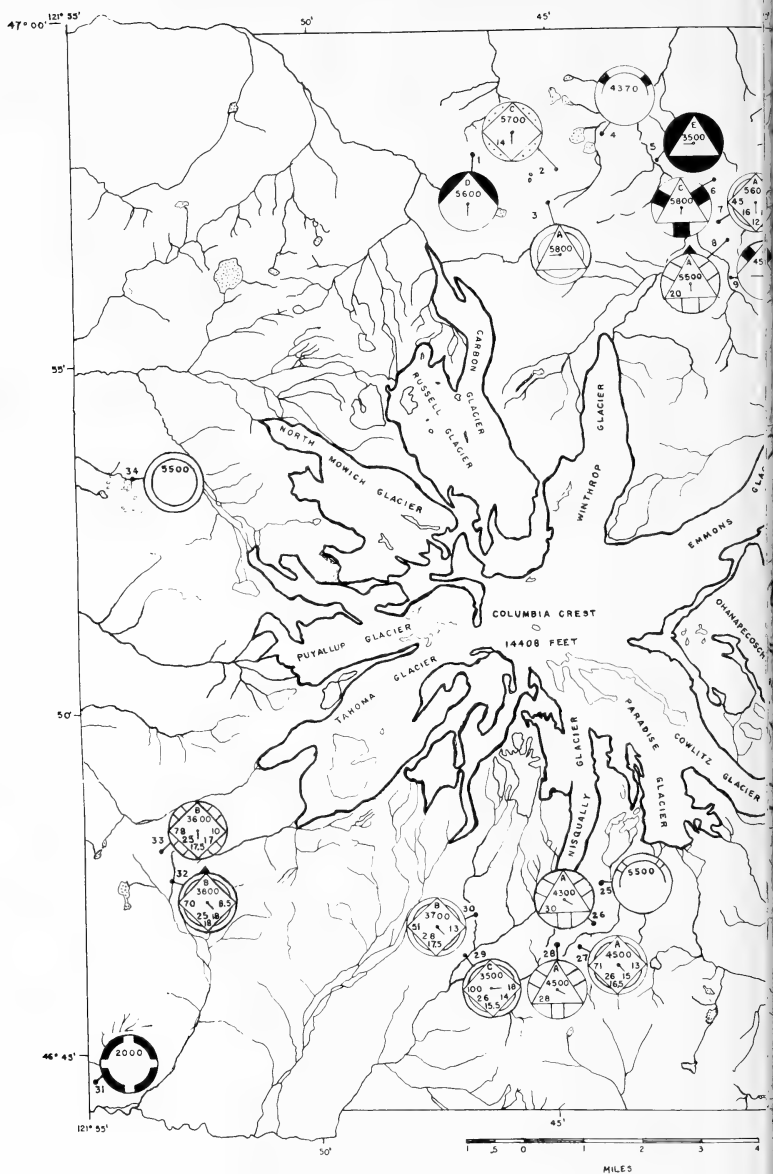


FIG. 3. Map of Mount Rainier National Park showing distribution of *Xerophyllum tenax* (based on observations and reports in 1955). The stations, numbered clockwise beginning in the northwest, are represented by circles connected to black dots (the actual sites).

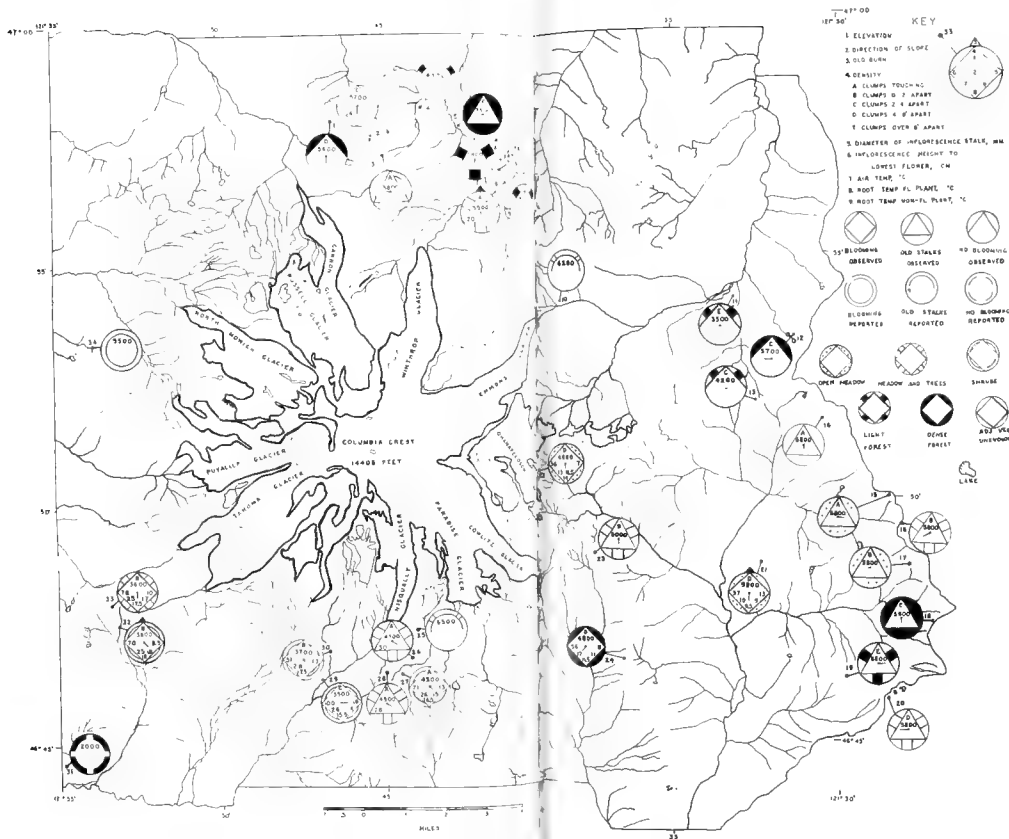


FIG. 3. Map of Mount Rainier National Park showing distribution of *Xerophyllum tenax* (based on observations and reports in 1955). The stations, numbered clockwise beginning in the northwest, are represented by circles connected to black dots (the actual sites).

One or more study sites was established at each station. Traced from USCG topographic map, Mount Rainier National Park, Washington, 1954.

TABLE 1. DESCRIPTIONS OF FIELD STATIONS WHERE STUDY PLOTS OF XEROPHYLLUM TENAX WERE ESTABLISHED ON MOUNT RAINIER IN 1955

STATION No.	DATE	TIME	SLOPE	LOCATION, SNOW AND SOIL CONDITIONS
1	Aug. 2	3:30 p.m.	15° south	1 mile west Yellowstone Cliffs, North Loop trail; soil wet.
2	Aug. 2	3:15 p.m.	45° south	Yellowstone cliffs, North Loop trail.
3	Aug. 2	2:45 p.m.	10° west	Windy Gap, North Loop trail; large snow fields adjacent.
4	Aug. 2	11:30 a.m.		Lake James, North Loop trail; snow areas present.
5	(See Fig. 3)			
6	Aug. 1	3:45 p.m.	15° south and also gentle north	West slope Grand Park, North Loop trail; numerous snow fields nearby.
7	July 25	12:15 p.m.	10° south	South edge of Grand Park, North Loop trail; no snow.
8	July 25	12:00 m.	18° south	South edge of Grand Park, North Loop trail; snow fields present.
9	July 25	11:00 a.m.	25° west	1 mile north Berkeley Park shelter, North Loop trail; snow fields present.
10	July 25		18° east	Yakima Park.
11	Aug. 25	12:00 m.		White River Entrance Station.
12	Aug. 22	2:20 p.m.	south	Deadwood Lakes; very wet.
13	Aug. 22		south	Ghost Lake.
14	Aug. 23	9:00 a.m.	5° south	Cascade Crest trail.
15	Aug. 23	10:45 a.m.	45° east	"
16	Aug. 23	12:30 p.m.	southwest	"
17	Aug. 23	1:00 p.m.	40° west	"
18	Aug. 23	2:15 p.m.	south	"
19	Aug. 23	4:30 p.m.	west	Three Lakes-Ohanapecosh trail.
20	Aug. 23	2:45 p.m.	40° west	Cascade Crest trail.
21	Aug. 5	12:00 m.	5° south	Shriner's Peak Lookout.
22	Aug. 17	10:45 a.m.	18° south	0.5 mile south Panhandle gap, Won- derland trail; highest elevation at which flowering plants were found.
23	Aug. 16	2:45 p.m.	10° south	Cowlitz Divide, 1 mile south Indian Bar, Wonderland trail.
24	Aug. 16	10:15 a.m.	15° west	2 miles east Nickel Creek patrol cabin, Cowlitz Divide, Wonderland trail.
25	Aug. 25		south	Paradise Valley.

STATION No.		DATE	TIME	SLOPE	LOCATION, SNOW AND SOIL CONDITIONS
26	July	13	10:35 a.m.	12° southeast	0.1 mile below Canyon Rim; snow present; dry soil.
27	July	13	10:15 a.m.	30° south	Narada Falls.
28	July	12	10:30 a.m.	13° south	0.7 mile below Narada Falls; melting snow fields nearby, soil wet.
29	July	13	10:40 a.m.	12° east	1 mile below Christine Falls; soil dry.
30	July	13	10:50 a.m.	38° south	Christine Falls; only a few plants in bloom, all against rock cliff.
31	Aug.	31			Nisqually entrance.
32	July	17	3:30 p.m.	38° south	2 miles south of Round Pass, West Side road.
33	July	17	3:40 p.m.	55° south	2 miles south Round Pass, West Side road.
34	Aug.	17			Golden Lakes.

instance the surface was nearly level, and the plants had evidently spread over the crest of a small hill from a south-facing slope; they indicated no sign of present or past flowering.

It has been noted in former years by Mount Rainier Park rangers that *X. tenax* increases greatly in numbers two to three years after a forest fire. Several competent observers related having seen it growing densely in old burns; these observations agree with those of the present writer.

A few factors that seemed to have relatively little effect on distribution definitely did appear to inhibit flowering. The one most obviously important in bringing about flowering during the 1955 season was the amount of light reaching the plant. Although old flowering stalks were found in dense forest as well as in open meadows in 1955, no plants were observed to bloom in dense shade. Instead, all flowering plants were confined to open meadows, light forests, or shrub-covered areas. Other limiting factors controlling flowering are probably temperature, especially of the soil, and, as will be evident later, the length and warmth of the growing season the previous year when the flower buds were being formed.

Soil temperatures about the roots at a three-inch depth beneath the clumps of flowering plants were between 0.5°–2.5°C. higher than those beneath non-flowering plants in the same vicinity. At only two stations were the root temperatures of flowering and non-flowering plants the same, and in no case was root temperature of the non-flowering plant found higher than the flowering one. Great care was taken to insure that the two plants studied at each station were on terrain of approximately the same amount of moisture, sunlight, etc. Perhaps the differences in recorded soil temperatures were due to slight differences in topography,

humus content of the soil, and qualitative and quantitative differences in the ground cover.

At most stations, no plants were seen flowering in 1955, although most plants retained old flowering stalks. At no time or place during the entire season were great displays of blossoms found, as had been reported in previous years. At the few stations where blossoms were present, only a few plants were involved and incidence of flowering did not seem especially related to density of spacing of clumps. Jepson (1901) has suggested that *X. tenax* blooms only once every seven years on Mount Tamalpais, Marin County, California. It is not likely that a similar flowering cycle exists on Mount Rainier. The 1955 season seemed to be the only season in several years in which *X. tenax* had not flowered heavily.

Inasmuch as flower-stalk elongation in this species begins in early summer, the 1955 flowering stalks were quite surely initiated during the 1954 growing season. Dr. A. W. Harrison of the University of Washington has observed the weather conditions on Mount Rainier for several summers. He reported (personal communication) that the summer of 1954 was one of the "poorest" during the last ten years, and that the last ten years have been below average in temperature, rainfall, and sunny days. In 1954 the snow disappeared at an elevation of 4500 feet on the south side of Mount Rainier one week later than in 1953 and four weeks later than in 1952. Probably the effectiveness of the growing season for *Xerophyllum* in 1954 was reduced by cooler temperature during the summer, as well as by the later start due to the persistence of the snow cover. It is quite probable that the length of the 1954 growing season was not long enough or warm enough to initiate many flower buds.

Department of Botany,
University of Minnesota, Minneapolis

REFERENCES

- FERNALD, M. L. 1950. Gray's manual of botany. 8th ed. American Book Co., New York.
- JEPSON, W. L. 1901. A flora of western middle California. Encina Publ. Co., Berkeley.
- . 1922. A flora of California. Vol. 1. Univ. Calif. Press, Berkeley.
- . 1951. A manual of the flowering plants of California. Univ. Calif. Press, Berkeley.
- JONES, G. N. 1936. A botanical survey of the Olympic Peninsula, Washington. Univ. Wash. Press, Seattle.
- MACOUN, J. 1888. Catalogue of Canadian plants. Vol. 2. Dawson, Montreal.
- PECK, M. E. 1941. A manual of the higher plants of Oregon. Binfords and Mort, Portland, Oregon.
- RYDBERG, P. A. 1900. Flora of Montana and Yellowstone National Park. New Era, Lancaster, Pennsylvania.
- SMALL, J. K. 1933. Manual of the southeastern Flora. Printed by the author, New York.
- SMILEY, F. J. 1921. A report upon the boreal flora of the Sierra Nevada of California. Vol. 9. Univ. Calif. Publ. Bot.

DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See Madroño 9:257-258. 1948.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
LILIACEAE				
* <i>Hesperocallis undulata</i> A. Gray	2n=24 II	H. Lewis, LA ¹	<i>Lewis</i> in 1952, LA	Borrego Valley, San Diego County, California
* <i>Nolina parryi</i> S. Watson	2n=20 II	H. Lewis, LA	<i>O'Donnell</i> in 1953, LA	Piñon Flats, Riverside County, California
* <i>Zigadenus brevibracteatus</i> H. M. Hall	2n=11 II	H. Lewis, LA	<i>Lewis</i> in 1950, LA	Red Rock Canyon, Kern County, California
RANUNCULACEAE				
* <i>Ranunculus occidentalis</i> var. <i>eisenii</i> A. Gray	2n=14 II	H. Lewis, LA	<i>Lewis</i> in 1955, LA	Mather, Tuolumne County, California
CRUCIFERAE				
* <i>Dithyrea californica</i> Harv.	2n=10 II	H. Lewis, LA	<i>Lewis</i> in 1955, LA	Borrego Valley, San Diego County, California
* <i>Erysimum capitatum</i> var. <i>bealianum</i> (Jeps.) Rossbach	2n=16 II	P. Raven, LA	<i>Mathias</i> 3027, LA	Kern County, California
* <i>Lyrocarpa palmeri</i> S. Watson	n=20	P. Raven, LA	<i>Lewis</i> in 1957, LA	Sentenac Canyon, San Diego County, California
* <i>Streptanthus inflatus</i> (S. Watson) Greene	2n=14 II	H. Lewis, LA	<i>Lewis</i> in 1957, LA	Temblor Range, Kern County, California
LINACEAE				
* <i>Cathartolimum digynum</i> (A. Gray) Small	2n=8 II	P. Raven, LA	<i>Lewis</i> in 1955, LA	Mather, Tuolumne County, California

(continued on p. 50)

* Prepared slide available.

¹ Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Third Edition, 1956, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
APOCYNACEAE				
* <i>Amsonia brevifolia</i> A. Gray	2n=22	C. Epling, LA	Lewis in 1940, LA	Quail Springs, San Bernardino County, California
* <i>Amsonia brevifolia</i> var. <i>tomentosa</i> (Torr. & Frem.) Jepson	2n=22	C. Epling, LA	Lewis in 1940, LA	Quail Springs, San Bernardino County, California
BORAGINACEAE				
* <i>Coldenia canescens</i> DC.	n=9	M. S. Cave UC	Raven 13122, UC	Kaibab Trail, so. rim of Grand Canyon, Coconino County, Arizona
* <i>palmeri</i> A. Gray	n=8	H. F. Chisaki, UC	Alava 1831, JEPS	27 miles south of Vidal, Riverside County, California
* <i>plicata</i> (Torr.) Coville	n=8	H. F. Chisaki, UC	Alava 1809, JEPS	Junction of highways 80-98 and road from Ogilby, Imperial County, California
* <i>purpusii</i> Brandeggee	n=9	H. F. Chisaki, UC	Moran 6320, UC	South of José María Aguirre, Nuevo Leon, Mexico
* <i>Cryptaniha pterocarya</i> (Torr.) Greene	n=12	H. F. Chisaki, UC	Raven 11723, UC	Gila Mountains, Yuma County, Arizona
* <i>Heliotropium parviflorum</i> L.	n=13	H. F. Chisaki, UC	Chisaki 1168, UC	San Blas, Nayarit, Mexico
* <i>Myosotis versicolor</i> (Pers.) Smith	n=12	H. F. Chisaki, UC	Alava 2295, UC	Pitkin Marsh, Sonoma County, California
VERBENACEAE				
<i>Glandularia perackii</i> Covas et Schnack	n=5	O. T. Solbrig, UC	Solbrig 2839, UC	Sierra de San Luis, San Luis Province, Argentina (grown at the U.C. Bot. Garden, Berkeley, Calif.)
<i>gooddingii</i> (Briq.) O. T. Solbrig ²	n=10	O. T. Solbrig, UC	Solbrig 2803, UC	Highway 66, 19.8 miles west of Seligman, Arizona

² *Glandularia gooddingii* (Briq.) O. T. Solbrig comb. nov. (*Verbena gooddingii* Briq., Ann. Conserv. & Jard. Bot. Genève 10:103. 1907.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>Glandularia canadensis</i> (L.) Small	n=15	O. T. Solbrig, UC	<i>Solbrig 2840</i> , UC	Cultivated at the U.C. Bot. Garden, Berkeley, Calif.
<i>Verbena bracteata</i> Lag. & Rodr.	n=14	O. T. Solbrig, UC	<i>Solbrig 2909</i> , UC	Highway 20, 12 miles west of Niles, Oregon
<i>prostrata</i> R. Br.	n=7	O. T. Solbrig, UC	<i>Chisaki, Sharsmith & Solbrig 2823</i> , UC	Hernandez, San Benito County, California
LABIATAE				
<i>Agastache urticifolia</i> (Benth.) Ktze.	2n=9 II	H. L. Wedberg, LA	<i>Lewis</i> in 1956, LA	Mather, Tuolumne County, California
* <i>Monardella cinerea</i> Abrams	2n=21 II	P. Raven, LA	<i>Raven 11197</i> , CAS	San Gabriel Mountains, Los Angeles County, California
* <i>Monardella lanceolata</i> Benth.	2n=21 II	H. Lewis, LA	<i>Lewis</i> in 1955, LA	Mather, Tuolumne County, California
* <i>Monardella linoides</i> A. Gray	2n=21 II	H. L. Wedberg, LA	<i>Raven 9327</i> , LA	Piute Mountains, Kern County, California
SOLANACEAE				
* <i>Chamaesaracha nana</i> A. Gray	2n=12 II	P. Raven, LA	<i>Lewis</i> in 1956, LA	Silver Lake, Mono County, California
* <i>Solanum xanthii</i> A. Gray	2n=12 II	H. Lewis, LA	<i>Levene</i> in 1949, LA	West Los Angeles, Los Angeles County, California
SCROPHULARIACEAE				
<i>Orthocarpus attenuatus</i> A. Gray	2n=12 II	H. Lewis, LA	<i>Lewis</i> in 1956, LA	Near Arvin, Kern County, California
<i>Orthocarpus linearilobus</i> Benth.	n=24	H. Lewis, LA	<i>Lewis</i> in 1956, LA	Near Arvin, Kern County, California
<i>Orthocarpus purpurascens</i> A. Gray	2n=12 II	H. Lewis, LA	<i>Lewis</i> in 1956, LA	Near Arvin, Kern County, California

(continued on p. 52)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
CUCURBITACEAE				
* <i>Marah macrocarpus</i> (Greene) Greene	2n=32 II	H. Lewis, LA	Lewis in 1950, LA	Santa Monica Mountains, Los Angeles County, California
COMPOSITAE				
* <i>Chaenactis Douglasii</i> var. <i>rubricaulis</i> (Stockwell) Ferris	n=6	R. O. Alava, UC	Bacigalupi & Alava 6497, JEPS	Converse Mountain, Fresno County, California
* <i>Chrysopsis foliosa</i> Nutt.	n=18	R. C. Jackson, KANU	Jackson 2464, KANU	Sandoval County, New Mexico
<i>Haplopappus ciliatus</i> (Nutt.) DC.	2n=12	R. C. Jackson, KANU	Richards 2648, KANU	Barber County, Kansas
* <i>Haplopappus divaricatus</i> (Nutt.) Gray	2n=10	R. C. Jackson, KANU	Richards 2055, KANU	Barber County, Kansas
* <i>Haplopappus hartwegii</i> (Gray) Blake	n=6	R. C. Jackson, KANU	Jackson 2465, KANU	San Juan County, New Mexico
* <i>Haplopappus pleuriflorus</i> (Gray) Hall	n=12	R. C. Jackson, KANU	Jackson 2507, KANU	Rio Arriba County, New Mexico
* <i>Machaeranthera gymnocephala</i> (DC.) Shinnars	n=5	R. C. Jackson, KANU	Jackson 2516-1, KANU	Otero County, New Mexico
<i>Machaeranthera tanacetifolia</i> (H.B.K.) Nees	n=4	R. C. Jackson, KANU	Jackson 2556, KANU	Socorro County, New Mexico
* <i>Ratibida tagetes</i> (James) Barnhart	n=16	R. C. Jackson, KANU	Jackson 2565, KANU	Bernalillo County, New Mexico
* <i>Ratibida columnaris</i> (Pursh) Raf.	n=14	R. C. Jackson, KANU	Jackson 2133, KANU	Otero County, New Mexico
* <i>Ratibida peduncularis</i> var. <i>picta</i> Gray	n=14	R. C. Jackson, KANU	Richards 564, KANU	Wilson County, Texas
* <i>Senecio longilobus</i> Benth.	n=20	R. C. Jackson, KANU	Jackson 2037, UNM	Bernalillo County, New Mexico
<i>Zinnia grandiflora</i> Nutt.	n=24	R. C. Jackson, KANU	Jackson 2002, UNM	Bernalillo County, New Mexico

TYPIFICATION OF PROSOPIS ODORATA TORR. & FREM. (LEGUMINOSAE)

LYMAN BENSON

Clarification of the concept of *nomina ambigua* and *nomina confusa* in the 1956 edition of the International Code of Botanical Nomenclature makes unnecessary my proposal (1941) that *Prosopis odorata* be included in the list of *Nomina confusa*. Article 66 (Lanjouw, et al., 1956) declares *nomina ambigua* to be illegitimate unless a satisfactory separation of the ambiguous elements can be made. If separation can be made clearly, one constituent must be designated as a lectotype. With this in mind, re-examination of the nomenclatural status of *Prosopis odorata* Torr. & Frem. (in Frem. 2nd. Rept. Expl. Exped. Rocky Mts., Ore., Calif. 313, pl. 1, 1845) is in order.

Three specimen sheets of the Fremont collection upon which *Prosopis odorata* is based are in the Torrey Herbarium, New York Botanical Garden. On each sheet there is a fallen fruiting spike with a cluster of fruits from the screw-bean, *Prosopis pubescens* Benth. The bulk of the material on each sheet consists of vegetative branches with spines, young leaves, and spikes of flowers of the western honey mesquite, *Prosopis juliflora* (Swartz) DC. var. *Torreyana* L. Benson. This mixture of material from two species resulted from collection of specimens in April when the mesquite was developing new leaves and was in flower. Probably the peculiar spiral pods were added from the ground. The two species often grow together along washes or in springy areas, and confusion may have arisen either in collecting specimens or in sorting them. The ambiguity of the type specimen of *Prosopis odorata* has been discussed as follows (Benson, 1941, pp. 753-754):

"Type collections: (1.) *P. odorata*, 'A characteristic tree in the mountainous part of northern [Alta] California, particularly along the Mohave [Mojave] and Virgin rivers [Virgin River in Nevada, Arizona, and Utah] the latter part of April.' According to Torrey, Pac. R.R. Rept. 4:82. 1855, the plant 'is *P. glandulosa* (in flower only), with the pods of *Strombocarpa pubescens*. The error arose from the mixing of specimens in Fremont's collections.' Torrey appended the following note to one of the three type sheets now in the New York Botanical Garden, 'I have scarcely a doubt that the leaves belong to *P. (Algarobia) glandulosa*—the fruit to *Stromb. pubescens*! I was led astray by Fremont placing the pods and the leafy specimens together—.' Interpretations of *P. odorata* have varied. Standley, Contr. U.S. Nat. Herb. 23: 353. 1922, in discussing the nomenclature of *P. juliflora* var. *velutina*, argued as follows: 'In case the plant should receive such recognition [as a species instead of a variety], the proper name for it is *Prosopis odorata* Torr. That name was based upon a flowering specimen of the present plant and fruit of *P. pubescens*, and for that reason has been discarded by most writers. Taking into consideration the specific name, 'odorata,' it seems reasonable to typify the name by the flowering specimen.' The branches with leaves and young flowers included in the type of *P. odorata* are neither *P. glandulosa* (i.e., *P. juliflora* var. *glandulosa*) as supposed by Torrey nor, despite the presence of a few hairs on the rachilla and secondary leaflets, *P. juliflora* var. *velutina* as supposed by Standley. Instead, they are *P. juliflora* var. *Torreyana*. Britton and Rose, N. Amer. Fl. 23: 183. 1928, took up the specific epithet *odorata* under *Strombocarpa* for the screw-bean. According to Article 64 of the In-

ternational Rules of Botanical Nomenclature, 'A name of a taxonomic group must be rejected if the characters of that group were derived from two or more entirely discordant elements, especially if those elements were erroneously supposed to form part of the same individual. A list of names to be abandoned for this reason (*Nomina confusa*) will form Appendix V' [not published]. The writer proposes that *Prosopis odorata* Torr. should be included in this list."

In the light of the 1956 rule, it is fortunate that in this instance segregation is clear and unmistakable, and the choice is easy. *Prosopis pubescens* Benth. (in Hook. Lond. Jour. Bot. 5:82. 1846) is established clearly in nearly all recent literature for the screw-bean, and changing the name by substituting *Prosopis odorata*, published one year earlier, is not desirable, even though this was done by Britton and Rose (loc. cit.). Furthermore, selection of the fruits alone for a lectotype would be less satisfactory than choice of the combination of twigs, leaves, and flowers. So long as *Prosopis juliflora* var. *Torreyana* is considered to be a variety, restriction of the type specimen of *Prosopis odorata* to include only the material from that population system will cause no nomenclatural upset. Therefore, the three sheets in the Torrey Herbarium of the New York Botanical Garden, the fruits excluded, are designated together as a lectotype of *Prosopis odorata* Torr. & Frem.

If the lectotype rule had been adopted before 1941, the writer would have recombined the epithet *odorata* in varietal rank under *Prosopis juliflora* (Swartz) DC. rather than to add the new epithet var. *Torreyana* to the nomenclature. Should var. *Torreyana* be elevated to specific rank, however, it must be known as *Prosopis odorata* Torr. & Frem.

Department of Botany,
Pomona College
Claremont, California

LITERATURE CITED

- BENSON, LYMAN. 1941. The mesquites and screw-beans of the United States. *Am. Jour. of Bot.* 28:748-754.
LANJOUW, J., ET AL. 1956. International Code of Botanical Nomenclature adopted by the Eighth International Botanical Congress, Paris, July 1954. Utrecht.

TWO NEW SPECIES OF *HELIANTHUS* FROM NEW MEXICO¹

R. C. JACKSON

During a field study of the New Mexican species of *Helianthus*, two new species were discovered. Morphologically they appear to be related to *Helianthus ciliaris* DC. but differ from this species in several diagnostic characteristics.

Helianthus heiseri sp. nov. Herba perennis 5-12 dm. alta; caulibus pluribus (vel unica) sparse strigosis, flavo-viridibus, striatis; foliis oppo-

¹ Field work for this study was supported by faculty research grants from the University of New Mexico.

sitis, sessilibus; laminis ad 7 cm. longis 2.3 cm. latis, cuneatis vel obtusis, acuminatis, serratis vel dentato-crenatis, ambis paginis strigosis resinosisque, nervis tribus conspicuis instructis; capitulis 1–3 in pedunculis 4–10 cm. longis; disco diam. 1.5–2.0 cm.; phyllariis lanceolatis, ciliatis, dorso levibus viridibusque, 2.6–3 mm. latis, 8–10 m. longis; radiis 16–20, 10–12 mm. longis; disci corollis 4–4.5 longis, basi flavis puberulentisque, lobis purpureis puberulentisque; receptaculi paleis acutis purpureis disci corollas aequantibus, earum apicibus acutis dorso plus minusve villosis; achaeniis ca. 3 mm. longis in maturitate nigris; pappis florum discorum aristis 2 lanceolatis instructis; pappis eorum radorum aristis 1–3 inaequalibus lanceolatis item instructis.

Perennial herb, 5–12 dm. high; stems one or several, sparingly strigose, yellowish-green, striate; leaves opposite, sessile, the blades up to 7 cm. long and 2.3 cm. wide, cuneate or obtuse at the base, acuminate at the tip, serrate or dentate-crenate on the margins, strigose and resin-dotted above and below, conspicuously 3-nerved; heads 1–3 on peduncles 4–10 cm. long; disc 1.5–2.0 cm. in diameter; phyllaries lanceolate, ciliate, smooth and green on the backs, 2.6–3.3 mm. wide, 8–10 mm. long; rays 16–20, 10–12 mm. long; disc corollas 4–4.5 mm. long, yellow and puberulent at the base, the lobes purple and puberulent; pales of the receptacle acute, purple, about equal with the disc corollas, the tips moderately villous on the backs; achenes about 3 mm. long, black at maturity; pappus of the disc of 2 lanceolate awns, the pappus of the rays of 1–3 unequal, lanceolate awns.

Type. New Mexico. Grant County: shallow ditch near the Mimbres River, elevation ca. 5400 feet, September 30, 1957, *Jackson 2521–1* (IND.) Isotype. *Jackson 2521–2* (UNM).

Additional specimens from the type locality are deposited in the herbaria listed above.

Thus far *H. heiseri* is known only from the Mimbres River Valley where it has been observed at several sites other than the type locality. This entity was probably responsible for Torrey's (1859) report of *H. grosseserratus* in "the valley of the Mimbres." The two species have several characteristics in common.

Helianthus crenatus sp. nov. Herba perennis 5–12 dm. alta; caulibus pluribus (vel unica), sparse strigosis, flavo-viridibus, striatis; foliis oppositis, sessilibus vel brevipedunculatis; laminis ad 9 cm. longis et 2.3 cm. latis, oblanceolatis, acutis, attenuatis, inaequaliter crenatis vel crenatolobatis insuper strigosis resinosisque, subtus strigosis vel strigoso-pilosis resinosisque, nervis tribus conspicuis instructis; capitulis 1–6 in pedunculis 6–13 cm. longis; disco diam. 1.8–2.4 cm.; phyllariis anguste lanceolatis, ciliatis, dorso in maturitate strigosis, aliquantulum patentibus, 2–3 mm. latis, 10–12 mm. longis; radiis 16–20, 10–12 mm. longis; disci corollis 5–5.7 mm. longis, basi flavis puberulentisque, lobis purpureis puberulentisque; receptaculi paleis quam disci corollis brevioribus, purpureis, dorso

ad apicem versus moderate villosis; acheniis ca. 3 mm. longis, in maturitate nigris; pappis florum discorum aristis 2 lanceolatis instructis; pappis eorum radiorum aristis 1-3 inaequalibus lanceolatis item instructis.

Perennial herb, 5-12 dm. high; stems one or several, sparingly strigose, yellowish-green, striate; leaves opposite, sessile or short petioled, the blades up to 9 cm. long and 2.3 cm. wide, oblanceolate, acute, attenuate at the base, unequally crenate or crenate-lobed on the margins, strigose and resin-dotted above, strigose or strigose-pilose and resin-dotted below; conspicuously 3-nerved; heads 1-6 on peduncles 6-13 cm. long; disc 1.8-2.4 cm. in diameter; phyllaries narrowly lanceolate, ciliate, strigose on the backs, somewhat spreading at maturity, 2-3 mm. wide, 10-12 mm. long; rays 16-20, 10-12 mm. long; disc corollas 5-5.7 mm. long, the base yellow and puberulent, the lobes purple and puberulent; pales of the receptacle shorter than the disc corollas, purple, acute, the tips moderately villous on the backs toward the apices; achenes about 3 mm. long, black at maturity; pappus of the disc of 2 lanceolate awns; the pappus of the rays of 1-3 uneven lanceolate awns.

Type. New Mexico. Sierra County: low area on the south side of Truth or Consequences, June 22, 1957, *Jackson 2504-1* (IND). Isotype. *Jackson 2504-2* (UNM).

Additional specimens are deposited in the herbaria listed above.

Helianthus heiseri and *H. crenatus* are closely related morphologically. The main diagnostic differences separating the two are apparent in the descriptions. In addition, the two species are separated by flowering dates. *Helianthus crenatus* reaches its maximum flowering period during the latter part of July, whereas *H. heiseri* reaches its peak from the middle to the latter part of September. Geographically the two species are separated by the Black Mountain Range.

It is quite possible that *H. crenatus* and *H. heiseri* may have been lumped with *H. ciliaris* DC. in the past. Some of the distinguishing characteristics are listed below in a comparison of the two new species with *H. ciliaris* as it occurs in the Rio Grande Valley of New Mexico.

	<i>H. ciliaris</i>	<i>H. heiseri</i>	<i>H. crenatus</i>
Stems	Mostly glabrous, glaucous	Sparingly strigose	Sparingly strigose
Leaves	Glabrous, bluish-green and glaucous	Strigose, light- or yellowish-green, resin-dotted	Strigose to strigose-pilose, light- or yellowish-green, resin-dotted
Phyllaries	Ovate, obtuse, erect appressed, glabrous or subglabrous on the back, ciliate, about 3.5 mm. wide, 5-7 mm. long	Lanceolate, acute, loose, glabrous on the back, ciliate, 2.6-3.3 mm. wide, 8-10 mm. long	Narrowly lanceolate somewhat spreading, strigose on the back, ciliate, 2-3 mm. wide, 10-12 mm. long

In the population of *H. crenatus*, several individuals not typical of the population as a whole were found. These plants were different from the

type in that some had long trichomes on the stem, the leaves were ashy grey, more heavily pubescent, and they apparently flowered earlier. Hybridization between *H. crenatus* and *H. ciliaris* may have been responsible for some of these variations, but generally they represent combinations not present in either species. Furthermore, Heiser and Smith (1955) have reported the chromosome number of *H. ciliaris* as $n=51$ (also $n=34$, Heiser unpublished) while the writer has found $n=17$ in *H. crenatus*. It may well be that these variations resulted from past hybridization with an unknown or now extinct species.

Department of Botany,
University of Kansas,
Lawrence, Kansas

LITERATURE CITED

- HEISER, C. B. AND D. M. SMITH. 1955. New chromosome numbers in *Helianthus*. *Proc. Indiana Acad.* 64:250-253.
TORREY, J. 1859. United States and Mexican Boundary survey. Part I, Botany of the Boundary. *Ex. Doc. No. 135*, 34th Congress, 1st Session, 27-259.
WATSON, E. E. 1929. Contribution to a monograph of the genus *Helianthus*. *Pap. Mich. Acad.* 9:305-475.

CHROMOSOME COUNTS IN THE SECTION *SIMIOLUS* OF THE GENUS *MIMULUS* (SCROPHULARIACEAE). III.

BARID B. MUKHERJEE AND R. K. VICKERY, JR.

This report¹ on the determination of chromosome numbers in the section *Simiolus* of the genus *Mimulus* is an integral part of a long range investigation into the taxonomy, genetics, and evolution of species in *Mimulus* (Vickery, 1951). Taken in conjunction with the previous counts (Vickery, 1955 and Mukherjee, Wiens, and Vickery, 1957), the counts reported here reveal a pattern of evolution in section *Simiolus* that involves both polyploidy and aneuploidy.

A slightly modified version of the technical method of Swaminathan, Magoon, and Mehra (1954) was found to produce better results than the methods previously used (Vickery, 1955 and Mukherjee, Wiens, and Vickery, 1957). Buds expected to contain anthers at the desired stages of microsporogenesis were killed and fixed for 24 hours in a mixture of two parts absolute ethanol and one part glacial acetic acid saturated with ferric acetate. Acetic acid was substituted for the propionic acid called

¹ This work was supported by the National Science Foundation. It forms a portion of the dissertation of the senior author submitted to the faculty of the University of Utah in partial fulfillment of the requirements of the Ph.D. degree. The authors wish to thank Drs. W.W. Newby and C. M. Woolf for their helpful criticisms of the manuscript.

for in Swaminathan, Magoon, and Mehra's schedule. Also, the buds were transferred after 24 hours to 70 per cent ethanol whereas their schedule called for leaving the buds in the fixative until used. The anthers were dissected out of the buds, smeared and stained in iron-aceto-carmin. Camera lucida drawings were made for each count and, in addition, photomicrographs were taken of the more intricate configurations. Each chromosome number reported is based on counts from an average of approximately ten microsporocytes. Herbarium specimens were prepared for each of the cultures studied. They will be deposited for future reference in the Garrett Herbarium of the University of Utah.

A total of eleven cultures was studied during the present investigation (table 1). The cultures include representatives of seven species and varieties of the section *Simiolus*: *M. guttatus* DC., *M. tilingii* Regel var. *tilingii*, *M. tilingii* var. *corallinus* (Greene) Grant, *M. glaucescens* Greene, *M. glabratus* var. *parviflorus* (Lindl.) Grant, *M. pilosiusculus* HBK., and *M. tigrinus* hort.

Of the five cultures of *M. guttatus* examined, three, (5003, 5007, and 5839) showed $n=14$ chromosomes. The configurations were regular and similar to those observed previously for other cultures of *M. guttatus* (Vickery, 1955, Mukherjee, Wiens, and Vickery, 1957). However, the two cultures of *M. guttatus* from Mather, California, exhibited frequent lagging chromosomes during the anaphase stage of the first meiotic division. Eight cells from three different plants of culture 5009 were observed at this stage of division. Two pairs of lagging chromosomes were found in each of two cells, one pair in each of three cells and no lagging chromosomes in the remaining three cells. In addition, two cells from two different plants of the other Mather culture, 5010, were observed at the first anaphase stage of meiosis. These cells each contained a single pair of lagging chromosomes. The cause of the lagging chromosomes was not clear from the configurations studied. Observations of five cells in the first telophase stage of division revealed that in one case the lagging pair of chromosomes was not being included in either nucleus whereas in the other four cases, both members of the pair were being included in one nucleus producing 15 to 13 segregations of the chromosomes. Observations of cells in the second metaphase stage of division confirmed the reality of these irregular segregations and indicated that, apparently, in a few cases, two pairs of lagging chromosomes had been included in the same daughter nucleus. Of such 16 to 12 segregations, only cells with 16 chromosomes were actually observed. Perhaps the number of cells studied was too small a sample to detect cells with 12 chromosomes which may be less viable than cells with 13 or more chromosomes. Of the 22 configurations of second metaphase chromosomes observed in microsporocytes of three plants of culture 5009, three contained 14 chromosomes, twelve contained 15, five contained 13, and two contained 16. Of twelve configurations of second metaphase chromosomes observed in microsporocytes of plants of culture 5010 five contained the normal number of 14 chromosomes, four

TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS

n = 14	<i>M. guttatus</i> DC. Pescadero, San Mateo County, California, altitude 20 feet, <i>Clausen</i> 2083 (5003). Yosemite Junction (marsh), Tuolumne County, California, altitude 1,350 feet, <i>Hiesey</i> 559 (5007). Big Cottonwood Canyon, Salt Lake County, Utah, altitude 7,100 feet, <i>Vickery</i> 334 (5839). <i>M. glaucescens</i> Greene Richardson Springs, Butte County, California, altitude 600 feet, <i>F. W. Pennell & A. A. Heller</i> 25667 (5653).
n = 14 ± 1 or 2	<i>M. guttatus</i> DC. Mather (meadow), Tuolumne County, California, altitude 4,600 feet, <i>Hiesey</i> 571 (5009). Mather (spring area), Tuolumne County, California, altitude 4,800 feet, <i>Hiesey</i> 569 (5010).
n = 15	<i>M. tilingii</i> Regel <i>tilingii</i> Mount Timpanogos, Utah County, Utah, elevation 7,800 feet, <i>Del Wiens</i> , Aug. 6, 1956 (5967).
n = 24	<i>M. tilingii</i> var. <i>corallinus</i> (Greene) Grant Porcupine Flat, Mariposa County, California, altitude 8,000 feet, <i>Hiesey</i> 576 (5011).
n = 32	<i>M. tigrinus</i> hort. Commercial seeds from F. Kirchhoff and Co., Johannesburg, South Africa (5056).
n = 45	<i>M. glabratus</i> var. <i>parviflorus</i> (Lindl.) Grant Illapel, Coquimbo, Chile, altitude 4,000 feet; Plant Introduction Service no. 144534, USDA (5041).
n = 46	<i>M. pilosiusculus</i> HBK. Botanic Garden, Copenhagen, Denmark (wild in Argentina, Chile, and Peru); Plant Introduction Service no. 181130, USDA (5320).

contained 15, one contained 13 and two contained 16. Thus, in the Mather cultures irregular meioses occurred in more than 50 per cent of the microsporocytes and a comparable proportion of aneuploid microspores was produced. If the resulting aneuploid gametes are functional, even occasionally, they might lead to the formation of aneuploid plants or populations. If such gametes are generally non-functional, they might help to explain the marked self and cross sterility observed in the Mather cultures in comparison to the relatively high self and cross fertility of other cultures of *M. guttatus* (Vickery, in press).

Mimulus glaucescens (5653) is morphologically closely related to *M. guttatus* (Pennell, 1951). It has $n=14$ chromosomes which are indistinguishable in appearance from those of *M. guttatus* (fig. 1). This investigation revealed no cytological basis for the strong crossing barrier (Vickery, 1956) that separates *M. glaucescens* from *M. guttatus* and its related species.

Mimulus tilingii var. *tilingii* (culture 5967) from a population growing on Mount Timpanogos of the Wasatch Mountains, Utah, generally has $n=15$ chromosomes in contrast to other Utah and California populations

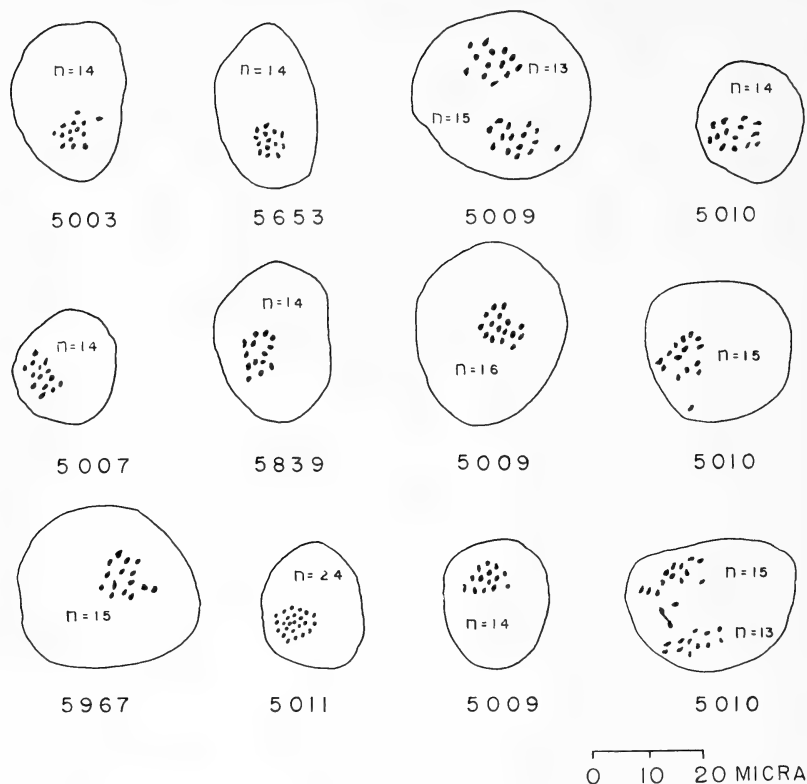


FIG. 1. Meiotic chromosomes of North American *Mimulus*: *M. guttatus*, 5003, 5007, 5009, 5010, 5839; *M. glaucescens*, 5653; *M. tilingii* var. *tilingii*, 5967, var. *corallinus*, 5011. All cells are in or near second metaphase except 5007, 5011, and 5967 which are in first metaphase. (Camera lucida drawings, $\times 645$.)

of that variety which have $n=14$ (Vickery, 1955 and unpublished). Various stages of meioses were examined in 16 microsporocytes from three different plants of culture 5967. Two of the cells contained 13 and 14 chromosomes instead of the more prevalent 15. However, *M. tilingii* var. *tilingii* did not show irregular numbers nearly as frequently as did the Mather populations of *M. guttatus*.

Mimulus tilingii var. *corallinus* (culture 5011) is closely related morphologically to *M. guttatus* and to *M. tilingii* var. *tilingii* (Grant, 1924) but is effectively separated from them by genetic barriers (Vickery, 1956). Culture 5011 forms sterile hybrids with *M. guttatus* and will not hybridize, despite numerous attempts, with *M. tilingii* var. *tilingii*. *Mimulus tilingii* var. *corallinus* has $n=24$ chromosomes in contrast to the $n=14$ of *M. guttatus* and the $n=14$ and $n=15$ of *M. tilingii* var. *tilingii*. Further work is in progress to try to establish the chromosome homologies

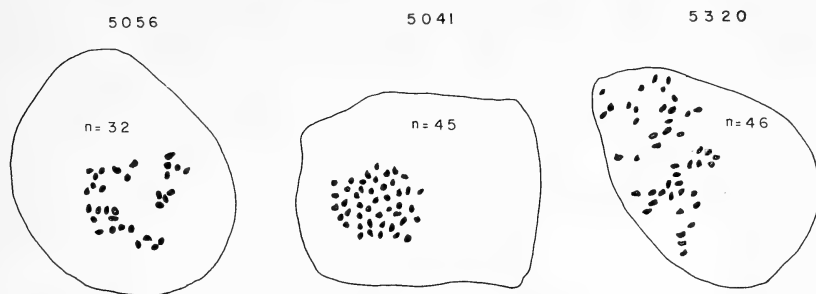


FIG. 2. Meiotic chromosomes of South American *Mimulus*: *M. tigrinus*, 5056 (first metaphase); *M. glabratus* var. *parviflorus*, 5041 (second metaphase); *M. pilosiusculus*, 5320 (second metaphase). (Camera lucida drawings, $\times 1134$.)

and the genetic relationships of the various entities within the *Mimulus tilingii* complex.

The three species from South America used in this study have higher chromosome numbers than any of the North American forms determined thus far. *Mimulus glabratus* var. *parviflorus* (culture 5041) from the Andes Mountains of Chile has $n=45$ chromosomes and *M. pilosiusculus* (culture 5320), originally from southern South America, has $n=46$ (fig. 2). *Mimulus tigrinus* hort., a cultivated derivative of *M. luteus* L. (Miller and Bailey, 1947) has $n=32$ chromosomes (fig. 2) which agrees with the report of Brozek (1932).

In conclusion, this survey of chromosome numbers and behavior in section *Simiolus* indicates that in general the chromosome number for *M. guttatus* is $n=14$. However, aneuploid microspores are produced with a frequency of greater than 50 per cent in the two cultures of *M. guttatus* from Mather. Such microspores, if functional even occasionally, might lead to the production of aneuploid plants or populations of *M. guttatus* similar to the aneuploid populations found in *M. tilingii* var. *tilingii*, *M. glabratus* var. *utahensis* and in the *M. glabratus* var. *parviflorus*—*M. pilosiusculus* group. The high chromosome numbers found in the South American species indicate that polyploidy, as well as aneuploidy, plays an important role in the evolution of species in section *Simiolus*. Further work is in progress to elucidate the questions of the cytogenetic relationships and taxonomic status of several entities in section *Simiolus* which have been raised by the results of this investigation.

Department of Genetics and Cytology,
University of Utah,
Salt Lake City 12, Utah

LITERATURE CITED

- BROZEK, A. 1932. Mendelian analysis of the "red-orange-yellow" group of flower colors in *Mimulus cardinalis* Hort. Preslia 11:1-10.
GRANT, A. L. 1924. A monograph of the genus *Mimulus*. Ann. Mo. Bot. Gard. 11: 99-388.

- MILLER, W. AND L. H. BAILEY. 1947. *in* The standard cyclopedia of horticulture by L. H. Bailey. MacMillan. Vol. 2, pp. 2054-2055.
- MUKHERJEE, B. B., D. WIENS, AND R. K. VICKERY, JR. 1957. Chromosome counts in section Simiolus of the genus Mimulus (Scrophulariaceae). II. Madroño 14: 128-131.
- PENNELL, F. W. 1951. *in* Illustrated Flora of the Pacific States by Leroy Abrams. Stanford University Press. Vol. 3, pp. 688-731.
- SWAMINATHAN, M. S., M. L. MAGOON, AND K. L. MEHRA. 1954. A simple propiocarmine PMC smear method for plants with small chromosomes. Indian Jour. Genetics and Plant Breeding 14:87-88.
- VICKERY, R. K., JR. 1951. Genetic difference between races and species of Mimulus. Carn. Inst. Wash. Year Book 50:118-119.
- . 1955. Chromosome counts in section Simiolus of the genus Mimulus (Scrophulariaceae). Madroño 13:107-110.
- . 1956. Data on interracial and interspecific hybridization in the section Simiolus of the genus Mimulus (Scrophulariaceae). Proc. Utah. Acad. Sci., Arts and Letters 32:45-64.
- (in press). Barriers to gene exchange within Mimulus guttatus (Scrophulariaceae).

REVIEW

Pollen and Spore Morphology/Plant Taxonomy. Gymnospermae, Pteridophyta, Bryophyta (Illustrations). (An Introduction to Palynology. II). By GUNNAR ERDTMAN. 151 pp., frontispiece, 5 plates, 265 figs. Almquist & Wilsell, Stockholm. 1957. \$8.00.

Over a period of more than 13 years, Gunnar Erdtman has undertaken the voluminous task of describing and illustrating representative pollen and spores of the world's plants. His contribution toward better understanding of the fundamentals of microspore morphology has given world-wide impetus to the development of this aspect of plant morphology and to palynology.

Erdtman's earlier publications were largely concerned with the pollen morphology of the more common angiosperms and gymnosperms in the experience of the Pleistocene pollen-analyst. Pollen workers, 10-15 years ago, were generally satisfied with knowing the gross morphologic features and key characteristics of pollen of the common wind-pollinated genera. Within the past few years, however, the boundaries of pollen work have been vastly expanded. The need for a thorough understanding of the pollen morphology of living plants has become increasingly apparent in identification and interpretation of fossil pollen, as well as a basis for the application of pollen morphology to systematic studies. Need for clarification of many of the details of microspore morphology and knowledge of pollen and spores of increasing numbers of plants has been answered in part by two volumes recently published by Erdtman. "An Introduction to Palynology. I. Pollen Morphology and Plant Taxonomy. Angiosperms" appeared in 1952. The volume being reviewed, "An Introduction to Palynology. II.", comprises the illustrations to the text of a treatise (Vol. III) on the morphology of microspores of the gymnosperms, pteridophytes and bryophytes which will be published at a later date.

Volume II includes "palynograms" (diagrammatic drawings showing the gross morphology of the grains as well as details of the surface pattern and exine stratification), a few photomicrographs and some electron micrographs of thin sections through spore walls of representatives of 12 gymnosperm families, 29 pteridophytic and 63 bryophytic families (23 Hepaticae and 40 Musci). Also included are similar illustrations for the surface pattern of, and optical sections through, the megaspore

membrane of a few members of the Cupressaceae, Pinaceae and Podocarpaceae among the gymnosperms and the Isoetaceae, Pilulariaceae and Selaginellaceae among the pteridophytes. The illustrations are arranged in sections dealing with each of the major groups: Gymnospermae, Pteridophyta and Bryophyta. Within each section the figures are placed alphabetically by genus. Reference to the family to which each genus belongs is made only at the beginning of the section. Spore palynograms of the Hepaticae and Musci are ordered alphabetically without regard to their class within the Bryophyta. This treatment makes for much clumsiness in use of the book by other than one well informed with the taxonomy of each group, and is the most serious fault one may find with this publication. Part of the difficulty could have been overcome by cross-referencing all genera to family. An arrangement in conformity with an acceptable taxonomic hierarchy would have been far more satisfactory, however, in gaining understanding of the overall microspore morphology of a family in terms of the representatives illustrated, or in attempting to compare the spore morphology of related families. One other less serious criticism which might be leveled at this publication is that concerning the number of figures and plates (3 out of 5) which have appeared already in other publications which most palynologists and others interested in microspore morphology would have seen. Some 17 figures and plates, in large part, or the only illustrations for *Abies*, *Cedrus*, *Ephedra*, *Keteleeria*, *Picea*, *Pinus*, *Pseudolarix*, *Lycopodium*, *Ophioglossum*, members of the Hedwigiaceae, Schizaeaceae and Marattiales, have already appeared in one or both of two periodicals in 1954 and 1956: the *Svensk Botanisk Tidskrift* and *Grana Palynologica*. We might suggest that this material could have been supplemented by additional data for these genera or groups in the present publication which purports to be a survey of a large group of plants. While not serious, numerous other obvious errors impair slightly the usefulness of this publication. There is no reference to illustrations of members of the Podocarpaceae (Gymnospermae) other than to one figure of the megaspore membrane of *Dacrydium cupressinum*. Microspores of six podocarpaceous genera are figured. Family references have also been omitted from the lists prefacing sections on Pteridophyta and Bryophyta for *Negripteris incana* (fig. 148, p. 81); *Oleandra neriiiformis* (fig. 150, p. 81); *Athalamia nana* (fig. 196, p. 101); *Brachiolejeunia sandwicensis* (fig. 198, p. 102); and *Southbya stillicidiorum* (fig. 245, p. 121). Other errors include absence of page numbers for some figures, or mistakes in page numbers for figures and plates.

A brief Introduction discusses exine morphology and the nature of the bladder among the winged (or saccate) gymnosperms (members of the Pinaceae and Podocarpaceae). Some of the terminology used was introduced and defined in the earlier, 1952, publication. Other terms (mesosaccia, aposaccia, cristae marginales, etc.) are apparently newly introduced further to confuse the already over-termed pollen morphologist. A twenty-two page supplement, containing technical articles by B. M. Afzelius and J. Radwan Pragłowski on electron microscopy and cutting ultra-thin sections as an aid to study of exine stratification, completes this publication. Pragłowski's article is simply and well presented and well illustrated, and is very welcome to those desiring to undertake the sectioning of pollen grain exines.

It is unfortunate that Vol. II has been published without the proposed accompanying text. The appearance of Vol. III, hopefully in the near future, will be awaited with interest.—JANE GRAY, Geochronology Laboratories, University of Arizona, Tucson.

NOTES AND NEWS

THE OCCURRENCE OF *PILOSTYLES THURBERI* (RAFFLESIACEAE) IN CALIFORNIA. In various articles and manuals relating to the vegetation of Arizona and California the suggestion has been made that *Pilostyles thurberi* Gray may occur in the desert areas of southern California. Never, as far as I am aware, has a documentation of this

range extension been published. The plant, parasitic on the branches of *Dalea emoryi* Gray, seems to be an exceedingly elusive one, as it is rarely collected. Only the minute flowers erupt from the host bark, the vegetative body being completely internal.

It is therefore worthwhile to confirm its occurrence in California. The following specimens, all from the Colorado Desert region of California, leave no doubt as to the presence of the parasite in the state: *Goodding* 43-19, 57 miles south of Indio (UC 690661), *Goodding*, 50 miles south of Indio (UCLA), *Wilson*, 30 miles west of El Centro (POM 273347), *Wilson*, near Ocotillo (RSA 43067). All these collections were on *Dalea emoryi*. On a field trip in 1958 I was unable to locate the parasite in any of the California localities. Because of agricultural developments it may not have survived in some of its known California and Arizona sites (perhaps including the type locality in Yuma County, Arizona). It still exists at Wellton, Yuma County, where it grows along the highway (*Kuijt* 1490, UC).

Pilostyles thurberi is the only species of the Rafflesiaceae in California. The other species of *Pilostyles* show an extraordinary geographical distribution. Some are found in Texas and northern Mexico, others in Chile, in Iraq, in Ethiopia, or in southwest Australia. The hosts are invariably leguminous shrubs growing in desert areas.—JOB KUIJT, Department of Botany, University of California, Berkeley.

NOTES ON THE FLORA OF ARIZONA.—Four interesting collections have come to the herbarium of the University of Arizona for identification during the past year. Of these two are genera new to the state, and two represent second collections of species rare in Arizona. Only one is a foreign weed.

Echinodorus berteroi (Spreng.) Fassett (Alismaceae) was collected 1½ miles north of Imperial Dam in the Imperial National Wildlife Refuge, Yuma County, by Gale Monson. It is a new generic record for Arizona, but one that might be expected. *Echinodorus berteroi* ranges from southern California eastward to the West Indies, but, according to Fassett's citation of specimens (Fassett, N. C. 1955. *Echinodorus* in the American Tropics. *Rhodora* 57:133-212), this is the first collection from the Colorado River as well as the first from Arizona.

Cardiospermum halicacabum L. (Sapindaceae), also a genus new to Arizona, was collected by L. N. Goodding and Richard Hevly on a rocky slope in the Coyote Mountains, Pima County. This new locality is about 50 miles north of the International Boundary, while the closest previous collection represented in the University of Arizona Herbarium is near Hermosillo, Sonora, Mexico, about 160 miles south of the border. Although *C. halicacabum* is cultivated as the "balloon vine," the rough, rocky area in which this specimen was growing precludes the possibility that it was an escape.

Beckmannia syzigachne (Steud.) Fernald (Gramineae), collected near Alpine, Apache County, was sent to the University of Arizona for identification by C. L. Isaacson, the county agricultural agent. This collection is the second for the state; the first having been made in 1951 by John Merkle at Greenland Lake, Grand Canyon National Park, Coconino County (Merkle, J. 1953. *Beckmannia Syzigachne* (Steud.) Fernald, New Record for Arizona. *Madroño* 12:32). The new collection is about 200 air miles southeast of the first.

Bupleurum rotundifolium L. (Umbelliferae) was brought to the herbarium for identification by a resident of Tucson, Pima County. It was growing in an unseeded, unfertilized section of a yard under an established elm tree (*Ulmus* sp.). This, also, is a second collection, the first having been made in Tucson by Toumey in 1892. Undoubtedly the new collection is a re-introduction of this Mediterranean weed, but the seed source is unknown.

Representatives of all of these collections are on file in the Herbarium of the University of Arizona.—CHARLES T. MASON, JR., Department of Botany, University of Arizona, Tucson.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954*).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$4.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany

University of California, Berkeley 4, California



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

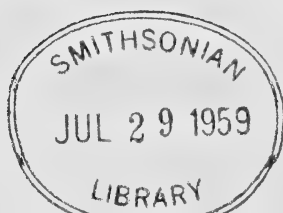
VOLUME 15, NUMBER 3

JULY, 1959

Contents

	PAGE
FACTORS AFFECTING THE DISTRIBUTION OF PONDEROSA AND JEFFREY PINES IN CALIFORNIA, <i>John R. Haller</i>	65
VIVIPARY IN <i>CORDYLINE AUSTRALIS</i> Hook., <i>Howard J. Arnott</i>	71
STUDIES ON SECOTIACEOUS FUNGI VI. <i>SETCHELLIO- GASTER</i> POUZAR, <i>Rolf Singer</i> and <i>Alexander H. Smith</i>	73
CEANOTHUS SEEDS AND SEEDLINGS ON BURNS, <i>Clarence R. Quick</i>	79
CHROMOSOME NUMBERS OF CALIFORNIA PLANTS, WITH NOTES ON SOME CASES OF CYTOLOGICAL INTEREST, <i>Richard Snow</i>	81
CHROMOSOME COUNTS IN THE GENUS <i>GAYOPHYTUM</i> , <i>David G. Dixon</i>	90
REVIEWS: Clara Chapman Hill, <i>Spring Flowers of the Lower Columbia Valley</i> (Robert Ornduff); Lloyd H. Shinners, <i>Spring Flora of the Dallas-Fort Worth Area, Texas</i> (Rogers McVaugh)	94
NOTES AND NEWS: <i>ALLIARIA OFFICINALIS</i> ANDRZ. IN OREGON, <i>Robert Ornduff</i>	96

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—WINSLOW R. BRIGGS.

Department of Biology, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: James R. Sweeney, San Francisco State College, San Francisco, California. First Vice-president: Baki Kasapligil, Mills College, Oakland, California. Second Vice-president: Henry J. Thompson, Department of Botany, University of California, Los Angeles, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: Winslow R. Briggs, Department of Biology, Stanford University, Stanford, California.

FACTORS AFFECTING THE DISTRIBUTION OF PONDEROSA
AND JEFFREY PINES IN CALIFORNIA

JOHN R. HALLER

Pinus ponderosa Dougl. and *P. jeffreyi* Murr. are among the most widely distributed forest trees in California and are well known to western botanists. They are very closely related, and various authors have treated them either as species (Sudworth, 1908; McMinn, 1951) or as varieties of a single species (Shaw, 1914; Jepson, 1925). However, after extensive field investigations (Haller, 1957) the details of which will be published elsewhere, I am convinced that *P. ponderosa* and *P. jeffreyi* are well defined species, and I shall treat them as such in this paper. All of the observations which follow are my own, unless otherwise noted, and were made in connection with the taxonomic study referred to above.

In California, *Pinus ponderosa* occurs from the Oregon border south along the Cascade Range and the western slope of the Sierra Nevada in an uninterrupted belt over 400 miles long and about 25 miles in width. Throughout this belt *P. ponderosa* is a conspicuous element in a forest rich in coniferous species. It is also common on the higher coastal-facing slopes of the mountains of southern California as far south as Cuyamaca Lake in San Diego County, and occurs sporadically in the Coast Ranges, especially north of San Francisco Bay.

The distribution of *P. jeffreyi* roughly parallels that of *P. ponderosa* in California, but *P. jeffreyi* is relatively more abundant in the south, and extends beyond the range of *P. ponderosa* into the higher mountains of northern Baja California, Mexico.

Although the ranges of *P. ponderosa* and *P. jeffreyi* in California nearly coincide in the broadest geographical sense, and although both are often found at the same locality, the two species characteristically occupy different habitats. *Pinus ponderosa* occupies the lower coastal-facing slopes of the mountains, whereas *P. jeffreyi* is usually found on the higher coastal or desert-facing slopes. The altitudinal ranges of *P. ponderosa* and *P. jeffreyi* shift gradually higher from north to south in California, just as do vegetation zones in general. However, the degree of shifting is not the same in both species. The lower limit of the *P. ponderosa* zone rises steeply from north to south. In the north, near Mount Shasta, the lower limit of *P. ponderosa* is about 1000 feet, but in the south, near Barton Flats in the San Bernardino Mountains, it is at 5000 feet (fig. 1). The upper limit of the *P. ponderosa* zone does not rise as steeply. It changes from about 5000 feet in the north to 7000 or 7500 feet in the south. Therefore, the altitudinal range of *P. ponderosa* contracts from about 4000 feet near Mount Shasta to little more than 2000 feet at Barton Flats. South of the Barton Flats area *P. ponderosa* becomes rapidly more infrequent in the

montane forest, until the most southerly stand is reached at Cuyamaca Lake, at the unusually low altitude of 4600 feet.

The lower edge of the *P. jeffreyi* zone rises from about 5000 feet near Mount Shasta to only a little over 6000 feet near Barton Flats (fig. 1). The zone in which *P. ponderosa* and *P. jeffreyi* overlap is consequently broader in the south than in the north, and stands comprised of both species are extensive near Barton Flats but highly restricted near Mount Shasta (Wiggins, 1940 and my own observations).¹ However, there are numerous localities throughout the state such as Shasta Valley in Siskiyou County and Pine Valley in southern San Diego County where *P. jeffreyi* occurs much lower, either with or without *P. ponderosa*, in what would usually be the lower portion of the *P. ponderosa* zone. The upper limit of *P. jeffreyi* rises from about 7500 feet near Mount Shasta to 9500 or 10,000 feet near Barton Flats. Thus the normal altitudinal range of *P. jeffreyi* increases from about 2500 feet in the north to 3500 or 4000 feet in the south.

What are the factors that cause this narrowing of the altitudinal range of *P. ponderosa* and broadening of the altitudinal range of *P. jeffreyi* in the south? There is both experimental and observational evidence which indicates that moisture at the lower altitudinal limit and temperature at the upper limit are usually the critical factors. Daubenmire (1943) has shown experimentally that seedlings of several important species of Rocky Mountain conifers, including *P. ponderosa*, are capable of withstanding much higher soil temperatures than those in their natural environments, but that they quickly succumb to drought conditions more severe than those in their natural habitats. In most areas of California also, *P. ponderosa* is probably restricted at its lower limit by moisture rather than temperature or some other factor. *Pinus ponderosa* is rarely found in areas with less than 25 inches of annual precipitation except near permanent sources of water. Of course moisture alone may not always be the limiting factor at low elevations. For example, in some localities where precipitation is still adequate but almost limiting, *P. ponderosa* might be held in check by its inability to compete with the more xeric chaparral vegetation. Billings (1950) has described the interesting occurrence of *P. ponderosa*, *P. jeffreyi* and other montane coniferous species on chemically altered andesitic soils in western Nevada. The climate of the area is too arid for these species under normal soil conditions, and supports only sagebrush or piñon-juniper vegetation. However, the sagebrush and most other shrubs cannot tolerate the chemically altered soils, and Billings has concluded that the absence of shrubby competitors enables the pines to persist.

The upward migration of *P. ponderosa* is, in all probability, usually

¹ Professor G. Ledyard Stebbins (personal communication) has observed extensive mixed stands of *P. ponderosa* and *P. jeffreyi* in the North Coast Ranges. The stands in this area apparently comprise an exception to the usual pattern of restricted mixed stands in the north and extensive ones in the south.

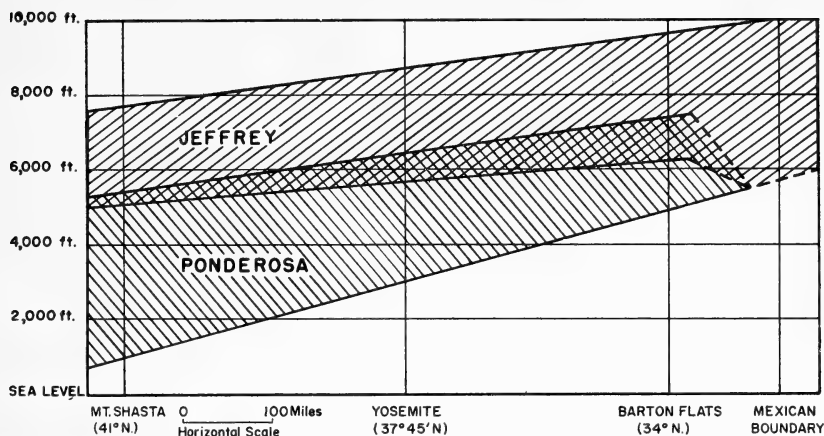


FIG. 1. Altitudinal distribution of *Pinus ponderosa* and *P. jeffreyi* along a north-south transect in California.

checked by low temperature. Californian *P. ponderosa* is killed by freezing when grown in areas with low winter temperatures, such as the Rocky Mountains (Weidman, 1939). I have observed frost damage on young individuals of *P. ponderosa* in California after periods of severe cold. The limiting effect of the low temperature undoubtedly works on the seedlings or young trees, because mature stands of *P. ponderosa* at its upper altitudinal limit are vigorous and show no evidence of being stunted.

Assuming that moisture and low temperature are the principal limiting factors for *P. ponderosa* at its lower and upper limits respectively, it is apparent from climatic data why *P. ponderosa* has a narrower altitudinal range in the south than in the north. As one travels south in California, precipitation generally decreases more rapidly than temperature increases at any given altitude (U.S. Weather Bureau, 1958). In other words, the isohyets gain altitude faster than the isotherms toward the south, leaving an ever shrinking zone that is favorable to the growth of *P. ponderosa*. It might be wondered, if the above is true, why *P. ponderosa* stops so abruptly in San Diego County rather than continuing toward the south over a decreased altitudinal range. There is no abrupt environmental shift at Cuyamaca Lake, and there are sites farther south that appear to be capable of supporting *P. ponderosa*. The reasons for the relatively sharp southern limit of the species may be historical. For example, a severe drought could have eliminated *P. ponderosa* south of where it occurs now, and the species may not yet have had sufficient opportunity to expand and reach its former extent.

Pinus jeffreyi is probably limited at the upper margin of its altitudinal range by a complex of factors all basically caused by low temperatures. Individuals growing near the upper limit of the species are often severely stunted in appearance, and obviously are showing the effects of the harsh

climate. In addition, the upper limit of *P. jeffreyi* almost exactly parallels that of *P. ponderosa* from north to south in California, suggesting that different degrees of the same factors are limiting both species at the upper margins of their altitudinal range (fig. 1).

The lower altitudinal limit of *P. jeffreyi* does not appear to be determined by any obvious physical factors, but rather by competition with *P. ponderosa* or other species. *Pinus ponderosa* grows faster under cultivation than *P. jeffreyi* in many diverse localities, from the Institute of Forest Genetics at Placerville, California (within the range of *P. ponderosa*), to England (Hooker, 1884). Near its upper limit *P. ponderosa* may not grow much faster than *P. jeffreyi* and thus permit the occurrence of mixed stands, but lower down, the more vigorous growth of *P. ponderosa* could exclude *P. jeffreyi* since both species have about equally high light requirements (Sudworth, 1908). The much greater extent of stands containing both species in southern California than farther north might be due to a slightly lowered vigor and subsequent lessening of the competitive ability of *P. ponderosa* in the south. In relatively dry southern California, *P. ponderosa* is in an environment where moisture is more likely to be limiting than in the north, and therefore might be expected to be less vigorous. The occurrence of *P. jeffreyi* in areas where *P. ponderosa* is lacking is further evidence of the limitation of *P. jeffreyi* by competition. In southern San Diego County, beyond the southern limit of *P. ponderosa*, *P. jeffreyi* often occurs through the entire altitudinal range of the montane forest. A short distance to the north, the lower portions of this forest are occupied by *P. ponderosa* instead. In the Sierra Nevada there are numerous sites within the montane forest, often at very low altitudes, such as sandbars in rivers or areas of serpentine soil, where *P. ponderosa* occurs infrequently if at all. The less demanding *P. jeffreyi*, however, is frequently encountered on these sites.

Revealing evidence concerning the distribution limits of *P. ponderosa* and *P. jeffreyi* has been obtained from east-west transects across the mountains as well as by north-south transects along their axes. As an example, I shall describe a west to east transect across the Sierra Nevada in the vicinity of Yosemite National Park in central California. The western and eastern slopes of the central portion of the Sierra Nevada display a striking series of contrasts, both topographically and climatologically. The western slope is fairly gradual, receives from 30 to 60 inches of precipitation annually in the montane forest belt (U.S. Weather Bureau, 1958), and has a relatively mild climate characterized by temperature extremes that are not pronounced. The eastern slope, on the other hand is very precipitous, receives only 10 to 20 inches of annual precipitation in the montane forest belt because of the rain shadow effect produced by the 13,000 foot crest that lies to the west, and has a continental climate with great extremes of temperature.

At the latitude of Yosemite (38° N.), the lowest continuous stands of *P. ponderosa* appear at an elevation of about 3000 feet, where the mean

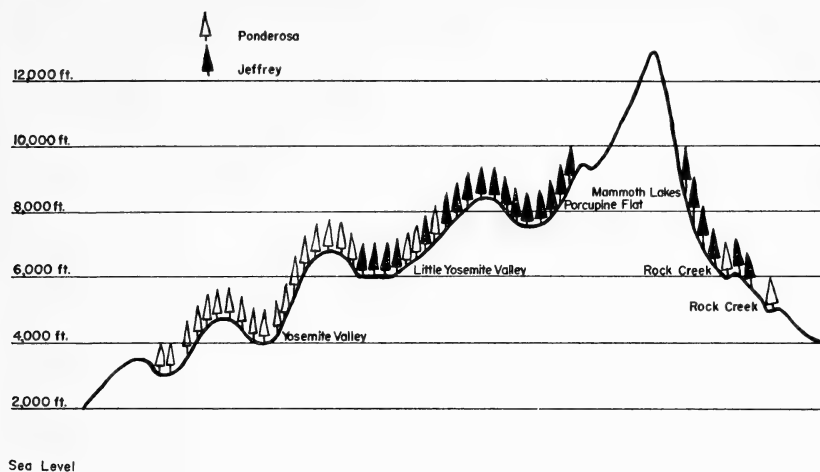


FIG. 2. Altitudinal distribution of *Pinus ponderosa* and *P. jeffreyi* along an idealized west-east transect across the central Sierra Nevada. Open triangles represent *P. ponderosa*; solid triangles represent *P. jeffreyi*.

annual precipitation is at least 30 inches. At about 6000 feet, *P. jeffreyi* is first found in abundance. The stands of *P. jeffreyi* growing at this relatively low altitude are usually not scattered at random over the slopes, however, but are concentrated near the margins of meadows or along streams, together with *Pinus contorta* subsp. *murrayana* Engelm., which occasionally occurs below its usual range in such places. *Pinus ponderosa* remains abundant for several hundred feet above the low places where *P. jeffreyi* is first encountered, especially on south-facing slopes, before giving way to *P. jeffreyi*. Above 6500 or 7000 feet, *P. jeffreyi* occurs alone and continues up to an elevation of approximately 9000 feet (fig. 2).

If the transect is continued across the 13,000 foot crest to the more arid eastern slope of the Sierra Nevada, *P. jeffreyi* will again be found below the 9000 foot elevation. Below 7000 or occasionally 6000 feet, where the annual precipitation may be as low as 10 inches, *P. jeffreyi* gives way to more xeric species, such as *Pinus monophylla* Torr. and *Artemisia tridentata* Nutt. *Pinus ponderosa* is not at all common on the eastern slope, and occurs without exception only along the banks of a few perennial streams. It is most abundant along Rock Creek near the Inyo-Mono county line at altitudes ranging from 5000 to 6500 feet (fig. 2).

The distribution pattern of *P. ponderosa* and *P. jeffreyi* along this west to east Sierran transect appears to be the result of the same limiting factors as those suggested by their north-south distribution. Although the lowest extensive stands of *P. jeffreyi* on the western slope of the Sierra Nevada are usually near meadows or along streams, the trees are prob-

ably not there because they need the moisture, but rather because *P. jeffreyi* is more tolerant of cold than is *P. ponderosa*. These low pockets where *P. jeffreyi* occurs are colder than the surrounding slopes in winter. The occasional presence of the usually subalpine *P. contorta* subsp. *murayana* in these pockets is further evidence of this fact. Probably *P. jeffreyi* merely tolerates the extra moisture present at its lowest localities, because, as already noted, the species occurs in much drier localities in other areas. In the harsh climate of the eastern slope of the Sierra Nevada, *P. ponderosa* survives only at low elevations where it is not too cold and along streams where it is not too dry. Where *P. ponderosa* and *P. jeffreyi* are found in the same general area on the eastern slope, the latter, in contrast to *P. ponderosa* often occurs both near the streams and on the adjacent slopes.

Pinus ponderosa is found in abundance on both sides of the Sierra crest from Lake Tahoe northward. However, in this region the crest of the range is much lower than farther south, and the environmental differences between the western and eastern slopes are not nearly as great. On the desert-facing slopes of the higher mountains of southern California, *P. ponderosa* is again restricted to unusually moist localities.

SUMMARY

Pinus ponderosa and *P. jeffreyi* are important components of the California montane forest. *Pinus ponderosa* generally occurs on the lower coastal slopes, while *P. jeffreyi* generally occurs on the higher coastal or interior slopes. The distribution of *P. ponderosa* is usually checked by lack of moisture at low altitudes and by low temperature at high altitudes. *Pinus jeffreyi* is also limited by low temperature at high altitudes, but at its lower margin the distribution of the species is apparently limited primarily by competition with *P. ponderosa*. The extensive mixed stands of *P. ponderosa* and *P. jeffreyi* in southern California where *P. ponderosa* may be less vigorous than in the north, might be the result of decreased competition from *P. ponderosa*. *Pinus jeffreyi* is more tolerant of extremes of low temperature and aridity than is *P. ponderosa*, and is at least equally as tolerant as *P. ponderosa* of extremes of high temperature and high moisture.

Department of Biological Sciences,
University of California at
Santa Barbara

LITERATURE CITED

- BILLINGS, W. D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. *Ecology*, 31:62-74.
DAUBENMIRE, R. 1943. Soil temperature versus drought as a factor determining lower altitudinal limits of trees in the Rocky Mountains. *Bot. Gaz.*, 105:1-13.
HALLER, J. R. 1957. Taxonomy, hybridization and evolution in *Pinus ponderosa* and *P. jeffreyi*. Doctoral dissertation, Univ. Calif., Los Angeles Library.
HOOKER, J. D. 1884. *Pinus jeffreyi*. *Gard. Chron.*, Dec. 27, 1884: p. 814.

- JEPSON, W. L. 1925. A manual of the flowering plants of California. Berkeley.
- McMINN, H. E. and E. MAINO. 1951. An illustrated manual of Pacific Coast trees. University of California Press, Berkeley.
- SHAW, G. R. 1914. The genus *Pinus*. Publ. Arnold Arboretum, No. 3.
- SUDWORTH, G. B. 1908. Forest trees of the Pacific slope. U. S. Government Printing Office, Washington, D.C.
- UNITED STATES WEATHER BUREAU. 1958. Climatological data. 1957 annual summary for the state of California. Vol. 61, no. 13.
- WEIDMAN, R. H. 1939. Evidences of racial influence in a 25-year test of *Ponderosa* Pine. Jour. Agr. Res., 59:855-887.
- WIGGINS, I. L. 1940. Yellow pines and other conifers observed in Lower California. Jour. N. Y. Bot. Gard., 41:267-269.

VIVIPARY IN CORDYLINE AUSTRALIS HOOK.

HOWARD J. ARNOTT

Vivipary is defined by Jackson (1928) as "... germinating or sprouting from seed or bud, while attached to the parent plant." Examples of vivipary are known in a number of genera of both the monocotyledons and dicotyledons. The classical example of this condition occurs in such mangroves as *Rhizophora mangle* Blanco. In this species when the seed germinates while still attached to the parent plant, the hypocotyl-radical elongates, forming a long sharp structure (Daubenmire, 1947, fig. 10, p. 64). When this seedling structure becomes heavy enough, it breaks away from the parent plant and drops into the mud below. Because this sharp hypocotyl-radical structure penetrates the mud the seedling often becomes anchored and is prevented from being washed away from its environment, especially in the intertidal zone.

In the Agavaceae of Hutchinson, of which *Cordyline* is one member, several genera have been reported to show vivipary. Both *Agave* and *Furcraea* are included in this category. The viviparous condition in *Furcraea* is a great deal different than that of *Rhizophora* or *Cordyline*. In *Furcraea* at certain points along the inflorescence bulbils are formed. These bulbils (aerial deciduous buds) consist of a series of papery and photosynthetic bud scales surrounding a short axis and a shoot apex. These structures are often formed in enormous numbers and literally cover the ground when they abscise from the parent inflorescence. Bulbils begin to grow immediately when proper conditions prevail; plants produced in this manner have a very rapid rate of early growth.

In a cultivated plant of *Cordyline australis* Hook. growing in Berkeley, California, many cases of vivipary were observed. The bright-green young seedlings were easily seen protruding out of the white fruits. A total of over fifty separate fruits were found exhibiting this character.

In most cases the cotyledonary arch and the first leaf were all that could be seen of the seedling outside the fruit. Two cases were observed in

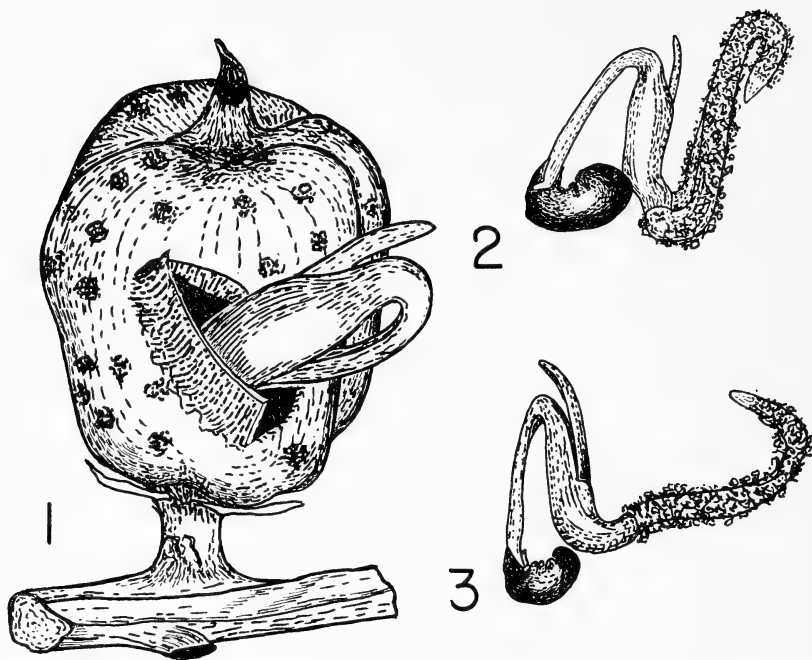


FIG. 1. Fruit of *Cordyline australis* Hook. showing a viviparous seedling protruding through the ruptured fruit wall. The fruit was still attached to the inflorescence. The densely stippled areas on the fruit represent the purple pigmented areas which normally occur on the white fruit of this species. $\times 9$.

FIGS. 2 and 3. Seedlings dissected from viviparous fruits showing the seed, the cotyledon, the first leaf, and the primary root. The primary root is intimately associated with the internal tissues of the fruit (see text). $\times 4$.

which the seed was pulled free of the fruit by the elongation and straightening of the cotyledon. Figure 1 shows a fruit in which the "aerial" parts of the seedling have protruded through the fruit wall. This protrusion was effected by a rupture of the tissues which enclosed the seed. The area surrounding the rupture seems to be at most only slightly discolored. In some cases dissection showed more than one seed to be present inside the fruit, but no cases of "multiple-vivipary" were found.

Figures 2 and 3 show seedlings dissected from "viviparous" fruits. The shiny black seed attached to the haustorial cotyledonary tip can be seen with the photosynthetic and sheathing parts of the cotyledon extending out in an inverted "U". Below the cotyledon is the axis and the primary root.

The most interesting point observed in these cases was the very intimate relationship between the internal tissues of the fruit and the primary root of the seedlings. This intimacy seems to be caused by the penetration of the internal fruit tissues by root hairs. When one tries to dissect these seedlings free of the fruit it is almost impossible to separate the primary

root from the internal tissues. It was not determined whether the root hairs grow between cell walls, into intercellular air spaces, or actually penetrate into the cells. The "fuzzy" appearance of the primary roots in figures 2 and 3 is an attempt to show this intimate association of the primary roots, root hairs, and internal fruit tissues after dissection.

One fact which seems to indicate that the root hairs are indeed the cause of this intimate association is that the root apex and some short distance behind it are completely free from any connection with the fruit tissues. This apparently is due to the absence of root hairs on such an immature part of the root.

Viviparous seedlings at a later stage than that shown in figure 1 have not been observed *in situ*. Such seedlings when removed from the fruit and placed on moist filter paper in a covered petri dish quickly show the production of new roots from the hypocotyl region. Apparently if these seedlings were planted they would produce normal plants.

While a number of cases of vivipary were found in this *Cordyline* plant, the number would be less than 0.1 per cent of the total number of fruits on the plant. One wonders what special physiological conditions were present in these viviparous fruits which caused or allowed the germination of these seeds. Also in the cases where more than one seed was present in a viviparous fruit, one wonders why only one seed germinated. One final question would be whether this condition occurs in this species in its native New Zealand, and what possible adaptive value might be found there for this condition, if it does occur.

Department of Biological Sciences,
Northwestern University, Evanston, Illinois

LITERATURE CITED

- DAUBENMIRE, R. F. 1948. Plants and environment. John Wiley & Sons, Inc., New York.
JACKSON, B. D. 1950. A glossary of botanic terms. Hafner Publishing Co., New York.

STUDIES ON SECOTIACEOUS FUNGI VI. SETCHELLIOGASTER POUZAR

ROLF SINGER AND ALEXANDER H. SMITH¹

As a result of studying the types of *Secotium tenuipes* Setchell, and *Secotium aurantium* Zeller, we believe it is logical to group these two in a single genus as designated in our title. They have the following characters in common: their spores are some shade of rusty ochraceous, have an imperfect but often distinctly discontinuous pore-region, are elongate in shape, and smooth or ornamented by plugs of material filling canal-like passages through the wall. The hyphae bear clamp connections at the

¹ Papers from the University of Michigan Herbarium and the Department of Botany, No. 1086, University of Michigan, Ann Arbor, Michigan.

cross-walls and the mature gleba does not become pulverulent. The outer layer of the peridium is a layer of enlarged to vesiculose cells. The hymenophoral trama (tramal plates of the gleba) is regular, but in the region next to the subhymenium it is composed of characteristically enlarged cells often taking the shape of sphaerocysts.

The subhypogeous habitat, its presence in the forest duff in mild climates, the presence of gastroid basidia and spores, and possibly the bright color (or the absence of pigment) in the peridium are also features of the genus, but these characters do not necessarily separate it too sharply from other secotiaceous genera.

The spore characters and the structure of the outer layer of the peridium are very distinct from those of *Secotium* as represented by the type, *S. gueinzii*, and do not allow these species to be placed in any other segregate of *Secotium*. The generic name *Setchelliogaster* was proposed by Pouzar for the type species (*Secotium tenuipes* Setchell) just after we had submitted for publication our own account in which a new generic name was proposed for the two species treated below; therefore we have had to adapt our paper to the use of Pouzar's name, *Setchelliogaster*.

SETCHELLIOGASTER Pouzar, *Ceská Mykologie* 12:33. 1958.

Spores varying from light brownish to dark rusty ochraceous, with a germ pore which is mostly distinct, more rarely imperfect (or at least spore wall at apex of spore partly discontinuous), elongate, smooth or with an ornamentation of the type of *Metraria insignis* (part of spore wall conspicuously heterogeneous consisting of a continuous wall through which extend minute canals plugged by a resinous substance, these plugs appearing as dots or lines or imperfect reticulation on the paler ground when spore surface is focussed upon); clamp connections present; peridium covered by an epithelium; hymenophoral trama regular but showing some inflated elements and sphaerocysts near the subhymenium. Peridium russet brown or orange or rarely ivory color; gleba brownish; columella percurrent; stipe not voluminous. Basidium-spore-configuration of the gastromycetoid type. Among thermophilous vegetation, growing subhypogaeously in humus under trees.

Type species of the genus: *Secotium tenuipes* Setchell.

SETCHELLIOGASTER TENUIPES (Setchell) Pouzar, *Ceská Mykologie* 12:34.

Figs. 1–3. 1958. *Secotium tenuipes* Setchell, *Jour. Mycol.* 13:239. 1907.

Gastrocarp 10–30 mm. tall, and 10–30 mm. broad, subglobose or broadly ovoid, subumbonate, at the base more or less truncate.

Peridium membranous in lower (marginal) portion, up to 1 mm. thick further up, and rather thick at the point of confluence with the columella, glabrous, not viscid, yellow-brown, deep brown (according to Setchell), or red-brown (“Morocco red” R. according to Zeller), usually dehiscent from the stipe-columella to expose a narrow ring of gleba.

Gleba variable in structure, loculate with very regular (in shape and position) chambers which become slightly lammellarly extended near the

exposed portion below, in other specimens generally with a gill-like structure especially visible in longitudinal sections of the gleba, and then consisting of anastomosing plates resembling those of *Polyporus alveolarius* but not in a regular manner and not permitting the shedding of spores, chambers sinuous or equal or completely irregular, gleba decurrent on the apex of the stipe-columella but for the most part dehiscent or free from the latter, ochraceous brown.

Stipe variable in length, reaching 20 mm., relatively thin, often bent or flattened, more or less concolorous with the pileus, striate, solid, equal or slightly attenuate downward, 2–3 mm. thick; columella continuous with stipe, percurrent and widened into the upper portion of the peridium, sometimes slightly narrowed before reaching the junction, lower portion to over half the lower length free from gleba; volva none; veil superior, arachnoid, transverse, scanty, evanescent after maturity is reached. Context fleshy, odorless.

Spores $14.5\text{--}19 \times 9.5\text{--}12.5 \mu$, ellipsoid to subovoid, shape in optical section slightly more ventricose on the outer line than on the inner one, but without a suprahilar appplanation or depression, and not so strongly asymmetric generally as in agaric spores, deep rusty ochraceous viewed in KOH, structure of wall complex at maturity and $1\text{--}1.2 \mu$ thick. Perisporium conspicuous and pale ochraceous-tawny. Exosporium heterogeneous, consisting of a continuous wall through which extend minute canals plugged by a resinous golden tawny substance, these canals at the surface of the perisporium appearing as dots or elongated irregular lines which may be fused to form an imperfect inconspicuous reticulation which appears tawny on a paler background, under mechanical pressure the combined exosporium and perisporium tending to separate from the episporium. Episporium tawny and appearing as a thin line. Endosporium interior to the episporium, thick and much paler in color than the latter. Spore apex complex and peculiar in structure: germ pore generally either poorly developed or absent but at times a perforation clearly visible, with a tawny-cinnamon, plug-like, thick, heterogeneous (different from wall-material) body in the region where the pores should be (abnormal spores often with 2–5 such structures), at times showing a slightly mucronate apical callus but no distinct perforation (a discontinuity of the wall strata may be observed only in the endo- and episporium), not truncate at apex, not necessarily germinating through the apex (lateral germination observed).

Basidia $30\text{--}40 \times 7\text{--}10 \mu$, (1–) 2– (3–)-spored, hyaline, numerous but rarely seen to form a large area of hymenium but rather intermixed with very numerous pseudoparaphyses, with a median constriction; sterigmata apical, straight or very slightly curved (not typically half-sickle-shaped but rather of gastroid type); pseudoparaphyses normally vesiculose and not projecting beyond the general level of the hymenium, hyaline, sometimes gigantic (cystidia?), about $32 \times 16 \mu$, generally $20\text{--}22 \times 13 \mu$; true cystidia or pseudocystidia none seen.

Subhymenium well-developed, subhyaline to hyaline, consisting of small irregular elements, some of them subisodiametric, forming a distinct if not very thick layer; hymenophoral trama consisting of brownish to brownish-hyaline hyphae of very variable diameter, some of them actually subisodiametric (e.g. 4–28 μ diam.), thin-walled or nearly so, some elements incrustated by deep rusty pigment, generally regular but chains of broad inflated elements alternating with strands of filamentous narrow hyphae, making the trama slightly intermixed, and reminding one of the gill trama of *Conocybe*. Peridial tissue thin, inner layer much like the hymenophoral trama, not gelatinous, its hyphae 5–27 μ broad; outer layer thick, its elements rusty brown from incrusting pigment, an epithelium or pseudoparenchyma consisting of spherocysts in chains or isolated, and few filamentous hyphae ending up (as a terminal member) in a spherocyst (spherocysts 8–28 (50) \times 8–22 μ) hyphae of all tissues with clamp connections.

Subhypogaeously on earth and humus under *Eucalyptus globulus*, *Quercus* sp., etc., in California, U.S.A., fruiting during the rainy season (November until April), in Oregon also in June.

Material studied. CALIFORNIA. Alameda County: University of California campus, Berkeley, Dec. 12, 1904, *Gardner* 229 (holotype, UC 221827), MICH. Topotypes: 25 March 1911, *Nichols*, MICH, NY (distributed as UC Herbarium Exsiccata 399); March 10 and April 11, 1911, *Harper*, NY; fall, 1923, *Parks*, NY; April 10, 1935, *Copeland* (det. E. E. Morse), NY; February and March, 1931, *Morse*, NY. Santa Clara County: Alma, March 2, 1919, *Parks* Z9, NY; Stanford University campus, March 5, 1942, *Cooke & Doty* 16619, MICH. Also material preserved at FH from same regions as above. OREGON: Corvallis, *Zeller*, NY.

Illustrations: Setchell (1907), pl. 107, figs. 4–8. Lloyd, *Myc. Notes* V:788, fig. 1184. Heim, *Rev. Myc.* 25:21. 1950. figs. 1–18.

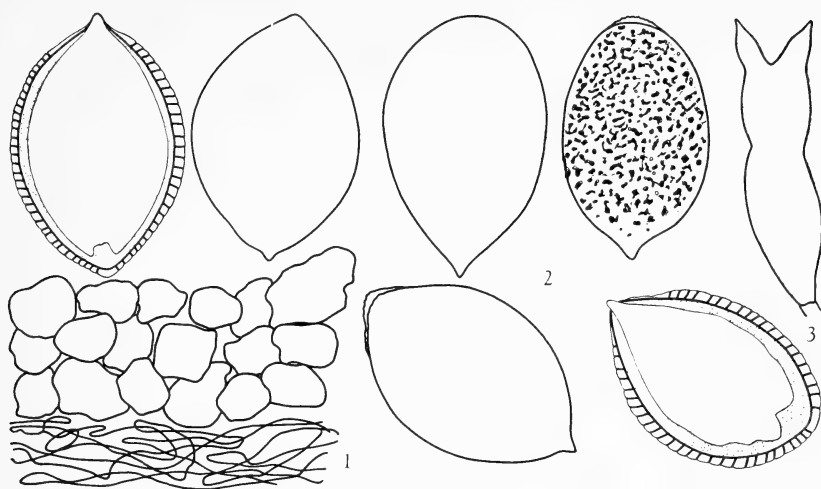
Setchell, in his original description, mentions the doubts he felt when publishing this species in *Secotium*: "In appearance and structure, this species varies so much from *S. Guenzii*, the type of the genus, that it may well be doubted whether it will ultimately be considered cogeneric with it, but, at present, it seems best to refer it to *Secotium* rather than attempt to split up that genus." We, on the other hand, find it rather amazing that between 1907 and 1957, in over half a century of mycological progress, no such attempt has been made.

Setchelliogaster aurantium (Zeller) Sing. & Smith, comb. nov. *Secotium aurantium* Zeller, *Mycologia* 39:292. 1947.

Gastrocarp 14 mm. broad, 15 mm. high, rounded umbonate above; peridium thin, not breaking from stipe-columella, bright orange, capucin yellow at base, gleba with small cavities, light brown.

Stipe terete, up to 3 mm. in diameter (about 20 mm. long), white, smooth, stuffed; columella also white, thin, percurrent; mycelium forming white rhizomorphs at base reminding one of those of the phalloids. Context white.

Spores 12–13 \times 7.5–8 μ , light brownish ochre, smooth, ellipsoid to ellip-



FIGS. 1-3. *Setchellioaster tenuipes*: 1, epicutis of peridium, $\times 450$; 2, spores, $\times 1000$; 3, basidium, $\times 450$.

soid-fusoid, with many tiny oil droplets inside, with moderately thickened wall composed of at least two layers, the outermost one well-colored, but perisporium not noticeable and no ornamentation seen, symmetric, with a distinct germ pore in a continuous wall showing lighter different material, but not distinctly showing an opening, and not truncate.

Basidia $21-22 \times 8.2 \mu$, with slightly oblique, conical, slightly curved sterigmata; pseudoparaphyses numerous, $19-20 \times 12.5 \mu$; cystidia none seen.

Hyphae of the hymenophoral trama hyaline, the mediostratum regularly arranged and consisting of a strand of parallel or subparallel rather broad axillary arranged hyphae, bordered on both sides by layers of spherocysts which become gradually smaller as the subhymenium and hymenium are approached, hyphae of the mediostratum $4-16.5 \mu$ thick, spherocysts about $28 \times 22 \mu$; peridium consisting of hyphous elements which are hyaline and $3-16 \mu$ thick, outermost layer of peridium divided from trama proper by a hypodermium-like layer which is not very sharply differentiated from both the outermost layer and the internal hyphous layer, but consists of spherocysts or broad swollen hyphae forming a pseudoparenchymatous tissue which, on its outer side carries a palisade of clavate to irregular, more or less erect to isodiametric elements with remarkably thick lemon-yellow walls (walls 1.5μ thick), the claviform ones about $22 \times 10 \mu$; all tissues with clamped hyphae.

On the ground, apparently in the forest, fruiting in summer, Cuba.

Material studied. Cuba, Santa Clara Prov. July 6, 1941, *W. L. White 803* (NY & FH), type.

This species differs from the other member of the genus in the structure of the spore wall which lacks any ornamentation, but the important character of the outer layer of the peridium places the species in this genus. The microscopic data given in the description are taken from the type, but most of the macroscopic data are from the original description.

There is no other genus of secotiaceous fungi known at present with a cellular outer peridial layer such as found in either of these two species. *Weraroa* has a different peridial structure and its spores have a broader truncate apex.

As for the affinities of this genus with representatives of the Agaricales, we would say that it is even more closely related to the family Bolbitiaceae than *Galeropsis* which lacks a cellular outer layer of the peridium. While the habit is definitely more reminiscent of *Conocybe* in *Galeropsis* than in *Setchelliogaster*, the latter has also some similarity with such species as the fleshier *Agrocybes*, *Conocybe intrusa*, etc. The species with ornamented spores may be compared with such forms as are now combined in the subgenus *Ochromarasmius* of *Conocybe* where there is also a somewhat protruding germ pore. As a smooth-spored species, *Setchelliogaster aurantiacum* would be comparable with some of the more thin-walled representatives of *Conocybe* such as have been described in Kühner's monograph. The color of the peridium in this species does not seem to be rare in *Conocybe*. Finally, the relatively voluminous hyphal elements making up the hymenophoral trama are distinctive both for this species and in *Conocybe* where they may serve as a generic character separating this genus from the neighboring genera of the family Bolbitiaceae. It may be added that careful observation always reveals the existence of numerous pseudoparaphyses in the hymenia of *Setchelliogaster* as well as in *Conocybe* and *Bolbitius*. The spores of *S. tenuipes* are sometimes observed to be forked or otherwise misformed or doubled. Such monstrosities are common in the genus *Conocybe* and also in some other bolbitiaceous genera.

In spite of all the congruence found between *Setchelliogaster* as a whole and the Bolbitiaceae as a whole, it cannot be denied that there are also features in this genus which recall similar features of agarics in other families such as the particular spore ornamentation of *S. tenuipes*. This remarkable structure was noticed by Singer (1951) and attention was drawn to the partly agaric-like characters. Although the species was then characterized as agaricoid, no attempt was made to link it up with any particular group of agarics, a task which has become easier now that more species of *Secotium* have become known more thoroughly.

The ornamentation of *Setchelliogaster tenuipes* is not exactly duplicated by any known bolbitiaceous species. It is found, with slight variations, in *Ganoderma* among the "polypores", and in widely separated species and groups of species of the Agaricales such as *Boletellus*, *Metarrhiza*, *Fayodia* (a genus considered as part of *Mycena sensu lato* by A. H. Smith), by a species described as *Tubaria thermophila* by Singer, and

another described as *Kuhneromyces alpinus* by Smith.² A similar spore type has been observed by us in the type of *Secotium eburneum* Zeller, but at present we do not wish to transfer that species to *Setchelliogaster* because the cellular layer of the peridium is overlaid by a layer of gelatinous filamentous hyphae forming a pellicle which is the outermost layer of the peridium.

LITERATURE CITED

- POUZAR, Z. 1958. Nové rody vyssich hub. II. Česká Mykologie 12(1):31-36.
- SETCHELL, W. A. 1907. Two new hypogaeous Secotiaceae. Jour. Mycology 13:236-241.
- SINGER, R. 1949. The Agaricales (mushrooms) in modern taxonomy. Lilloa 22:1-832, pls. 1-29.
- . 1955. Le Genre *Melanomphalia* Christianson. Rev. Mycologie 20:12-17.
- . 1957. New genera of Fungi X.—*Pachylepyrium*. Sydowia 11:320-322.
- ZELLER, S. M. 1941. Further notes on Fungi. Mycologia 33:196-214.
- . 1947. More notes on Gasteromycetes. Mycologia 39:282-312.

CEANOTHUS SEEDS AND SEEDLINGS ON BURNS

CLARENCE R. QUICK¹

Blue Canyon, the large rocky canyon of Big Creek, a tributary of Kings River, lies in the Sierra Nevada just southeast of Shaver Lake, Fresno County, California. This canyon once supported a magnificent stand of timber and in spots still does. Portions of the northerly part of the canyon were logged with "steam donkeys" around 1915. The ecologic course of reforestation on logged or burned forest areas, especially on high-quality forest sites, is often interesting and significant. Causes for variations in the reforestation process are not fully understood even yet.

The areas of Blue Canyon logged in 1915 were clear-cut, but somehow the methods used in the logging, the weather cycle after the logging, or perhaps other and unrecognized factors caused the cutover area to regenerate timber species promptly, especially sugar pine. For a while the new growing forest was somewhat brushy, but the brush slowly gave way to the competition of the trees, mostly pine trees, and by 1945 the old cutover area in the northeast corner of Blue Canyon was a beautiful stand of pole-sized sugar pine, ponderosa pine, white fir, and incense-cedar. Sugar pine predominated in much of the stand. Some decadent brush persisted, largely in the forest openings. On a one-acre study plot in the northwest corner of section 14, T10S, R25E, were found some 180 sugar pines, mostly pole-sized trees 4 to 12 inches in diameter.

¹ Pathologist at California Forest and Range Experiment Station, maintained at Berkeley, California, by the Forest Service, U. S. Department of Agriculture, in co-operation with the University of California.

² This latter seems to be congeneric with *Melanomphalia nigrescens* and *M. platen-sis*. Singer (1955) placed *Melanomphalia* in the Cortinariaceae, and (1957) proposed the combination *Melanomphalia alpina* (Smith) Sing.

One hot afternoon in August 1947 a sawmill near the bottom of Blue Canyon (at an altitude of about 3,500 feet) caught fire and burned. The fire escaped and spread over 4 to 5 square miles of forest in the north-eastern part of Blue Canyon. The fire was stopped near the rim of the canyon at an altitude of about 6,000 feet. The one-acre study plot was completely burned—all conifers and, for that matter, all plant parts above the ground surface were killed. Burned forest extended roughly for a mile in all directions from the plot.

In 1948 some small plots were established on the burned one-acre plot to see what plants were "coming back" on the burn. Ten separate milacre plots were distributed over the old one-acre plot. (A milacre—one-thousandth of an acre—is a square with sides of 6.6 feet.) Current-season seedlings which came up in the spring of 1948, the first spring after the burn, and resprouts from subsurface parts of plants which survived the burn were counted and recorded.

From the 10 milacres were removed 281 seedlings of Manzanita (*Arctostaphylos manzanita* Dudley), 1,204 seedlings of Sierra Nevada gooseberry (*Ribes roezli* Regel), and 1,994 seedlings of deerbrush (*Ceanothus integerrimus* H. & A.). This is a total of 3,480 seedlings of these three brush species on 10 milacres (1/100 acre).

From a single milacre were removed 83 manzanita seedlings; from another, 612 gooseberry seedlings; and from still another, 1,814 deerbrush seedlings. Subsequent checks of these milacre plots showed that no current-season seedlings of these three species came up in 1949 or in 1950. No conifer seedlings appeared on the milacre plots, and almost none within the boundaries of the old one-acre plot.

This ability to germinate suddenly after fire is characteristic of the seeds of several genera of shrubby plants in California; see, for example, Jepson (1925). Species which react in this way are commonly called fire-type plants. Seeds of firetype species are mechanically durable, long-lived, and come to be relatively ubiquitous in the forest floor of the Sierra Nevada. Quick (1956) has shown that large numbers of many kinds of seeds are "stored" in the duff even under virgin stands of timber. Quick (1935) has also shown that treatment in boiling water plus stratification will condition seeds of many species of *Ceanothus* L. for immediate germination.

The longest treatment in boiling water of the experiments reported in 1935 was 5 minutes. This treatment resulted in very satisfactory germination in some species, and it was obvious that the limit of tolerance of some collections was not closely approached. So the question arose, just how much exposure to boiling water, for example, will *Ceanothus* seeds endure?

To seek an answer, samples consisting of 100 airdry seeds of deerbrush and of mountain whitethorn (*Ceanothus cordulatus*) were treated in the Berkeley laboratory by tossing them into a screen sieve suspended in vigorously boiling tap water. After treatment, the sieve and seeds were removed from the boiling water, soused in cold water, planted in autoclaved river sand, stratified to obviate embryo dormancy, and germinated

in a greenhouse. Samples of seed collection Q#026 (deerbrush, collected on the South Fork of Stanislaus River at about 4,800 feet altitude) were treated in boiling water for 1 to 20 minutes. Twelve per cent of these seeds germinated after having been boiled for 20 minutes. Samples of seed collection Q#239 (mountain whitethorn, collected near Strawberry, Stanislaus National Forest, at about 5,400 feet altitude) were treated for 5 to 30 minutes in boiling water. Twenty-five per cent of these seeds germinated after being boiled for 25 minutes, but none germinated after being boiled for 30 minutes. A manuscript, now nearing completion, will analyze statistically the seed germination reactions of several species of *Ceanothus* with respect to seed age, altitude of seed collection, length of exposure to boiling water, and temperature and length of stratification treatment.

Many seeds, even *Ceanothus* seeds, are destroyed in any forest fire, but the above preliminary experiments suggest that seeds of many firetype plants are very durable, long-lived, and sufficiently resistant to high temperatures to escape destruction and to completely revegetate a heavy burn. Thus starts the first stage in a new cycle of forest development.

California Forest and Range Experiment Station,
University of California, Berkeley.

LITERATURE CITED

- JEPSON, WILLIS L. 1925. The life zones. *In* A manual of the flowering plants of California, pp. 4-8. Berkeley, California.
- QUICK, CLARENCE R. 1935. Notes on the germination of *Ceanothus* seeds. *Madroño* 3(3):135-140.
- . 1956. Viable seeds from the duff and soil of sugar pine forests. *Forest Science* 2(1):36-42.

CHROMOSOME NUMBERS OF CALIFORNIA PLANTS, WITH NOTES ON SOME CASES OF CYTOLOGICAL INTEREST

RICHARD SNOW

Meiosis has been examined in microsporocytes of various species of Californian plants, and the resulting chromosome numbers are listed in Table 1. During the course of these observations several meiotic phenomena have been observed that have cytological interest beyond chromosome number. These will be discussed briefly in order to point out some areas possibly worthy of further study.

METHODS. Buds were fixed in 1:3 acetic-alcohol for one to several days and stored in 70 per cent alcohol under refrigeration. After soaking in water for a few minutes the material was softened in 1N HCl at 60°C. for 5-10 minutes, rinsed with water, and the anthers squashed in aceto-orcein or aceto-carmin. The *Fritillaria* material was stained by the Feulgen reaction. Permanent slides were made by Bradley's (1948) method, without removing the coverslip.

TABLE 1. DOCUMENTED CHROMOSOME NUMBERS OF CALIFORNIA PLANTS¹

SPECIES	CHROMO- SOME No. (2n)	LOCALITY AND COLLECTOR
<i>Fritillaria biflora</i> Lindl.*	24+0-8ff	Near Saddle Peak, Santa Monica Mts., Los Angeles County, <i>Lewis</i> in 1958.
<i>Delphinium polycladon</i> Eastw.	16	Rodger's Lake, Tuolumne County, <i>Snow</i> 284.
<i>Ranunculus californicus</i> Benth.	28+f	Road from Bridgeport to Highway 140, Mariposa County, <i>Snow</i> and <i>Wedberg</i> in 1953.
<i>Eschscholtzia mexicana</i> Greene	12	15.3 miles north of Goffs on the road to Lanfair, San Bernardino County, <i>Snow</i> 18.
<i>Thelypodium lasiophyllum</i> (H. & A.) Greene	48	Red Rock Canyon, Kern County, <i>Snow</i> 410.
<i>Isomeris arborea</i> Nutt.*	40	2.7 miles west of Whitewater, Riverside County, <i>Raven</i> 11409. Point Dume, Los Angeles County, <i>Snow</i> (no specimen). Red Rock Canyon, Kern County, <i>Snow</i> 407.
<i>Lupinus superbus</i> Hel. var. <i>elongatus</i> (Greene) C. P. Smith*	48	Matterhorn Canyon, Tuolumne County, <i>Snow</i> 292.
<i>Astragalus Bolanderi</i> Gray	22	Badger Flats, near Huntington Lake, Fresno County, <i>Snow</i> 62.
<i>Astragalus leucopsis</i> (T. & G.) Torr.	22	Point Dume, Los Angeles County, <i>Raven</i> 13857.
<i>Astragalus oocarpus</i> Gray	22	4.6 miles north of Santa Ysabel, San Diego County, <i>Raven</i> and <i>Snow</i> 9557.
<i>Astragalus pomonensis</i> Jones	22	1.7 miles west of Dripping Springs Guard Station, Riverside County, <i>Raven</i> and <i>Snow</i> 9543.
<i>Astragalus crotalariae</i> Benth.	24	Salton Sea State Park, Riverside County, <i>Raven</i> 11484.
<i>Datisca glomerata</i> (Presl) Benth. and Hook.	22	Banning-Idyllwild Road near Grand View Guard Station, Riverside County, <i>Raven</i> and <i>Snow</i> 11115.
<i>Epilobium obcordatum</i> Gray	36	Little Slide Canyon, Mono County, <i>Snow</i> 275.
<i>Oenothera californica</i> Wats. var. <i>californica</i> *	28	11 miles east of Riverside, Riverside County, <i>Snow</i> and <i>Mosquin</i> 318.
<i>Gayophytum racemosum</i> T. & G.	14	Little Slide Canyon, Mono County, <i>Snow</i> 273.
<i>Monardella odoratissima</i> Benth.	42	Little Slide Canyon, Mono County, <i>Snow</i> 272.

¹ Voucher specimens and prepared slides are in the Herbarium of the University of California, Berkeley.

* See discussion in text.

f = fragment chromosome.

SPECIES	CHROMO- SOME No. (2n)	LOCALITY AND COLLECTOR
<i>Datura meteloides</i> DC.*	24	See Table 2.
<i>Plantago insularis</i> Eastw.	8	Near Red Rock Canyon, Kern County, <i>Snow</i> 416.
<i>Pedicularis groenlandica</i> Retz.	16	Pass between Little Slide Canyon and Slide Canyon, Tuolumne County, <i>Snow</i> 276.
<i>Proboscidea Jussieu</i> Keller	30	Putah Creek, west of Davis, Yolo County, <i>Snow</i> 605.
<i>Senecio Fremontii</i> T. & G. var. <i>occidentalis</i> Gray*	40+f	Little Slide Canyon, Mono County, <i>Snow</i> 270.

My thanks are due Dr. Harlan Lewis for the buds of *Fritillaria biflora*, and to Mr. Peter Raven for the material of *Astragalus crotalariae* and for permission to cite his unpublished observations on *Isomeris arborea*.

CYTOLOGICAL NOTES

FRITILLARIA BIFLORA. The fragments in this species are one-third to one-fourth the length of the long arms of chromosomes of the basic complement at anaphase II. It is not certain how constant their number is from plant to plant, since buds from several plants were fixed in the same vial. However, since this species has usually only two to four flowers per plant it is almost certain that each bud in a meiotic stage was derived from a different plant. The number of fragments found in various buds from this collection was 2, 4, 6, or 8. There was also occasionally a smaller variation in number from one PMC to another within the same bud.

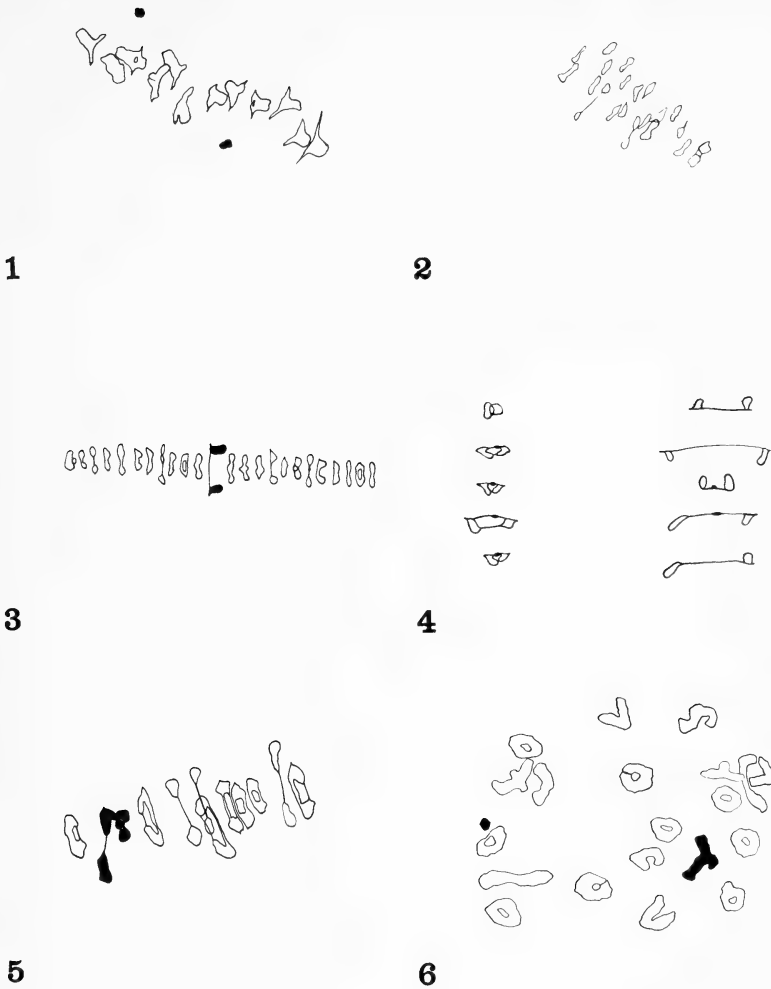
At metaphase I from 1 to 4 "fragment-pairs" have been seen in various buds (fig. 1), and no fragments have been seen at this stage which were not "paired." These dual associations may represent the synapsis of homologous fragments or the division of unpaired fragments. The few mitotic cells on the slides were not clear enough for a definitive answer. The fragments do not congress to the metaphase plate with the other bivalents, but instead usually lie off in the cytoplasm above or below it. Their position at metaphase I may account for their frequent inclusion in the daughter nuclei. However, lagging of the fragments is not infrequent at anaphase. At anaphase I a fragment-pair may separate, one or both halves being included in a nucleus; or the pair may be included, without separation, in one daughter nucleus. As a result of lagging and irregular separation, an anaphase nucleus may receive from none to as many fragments as the PMC contains. Anaphase II distribution is likewise variable. Irregularities of division possibly also occur in mitosis, and may account for the variation in the number of fragments observed in different PMCs of the same bud.

Anaphase observations suggest that the fragments probably possess a centromere, though one which is perhaps less efficient in division than normal. An area which is probably the centromere region appears sub-

terminal in mitotic cells. The preparations were not especially good for study of this feature, however, but certainly the fragments gave no indication of being isobrachial. They do not, therefore, appear to be products of mis-division of a centromere followed by the uniting of sister chromatids to convert a telocentric into an iso-chromosome, as has been found in the triploid *Fritillaria latifolia major* by Darlington (1940; see also Darlington, 1939). Whatever their origin it seems likely that all the fragments observed in the various buds (and hence from several plants) are the result of a single primary event of the past, both because their similar form and because the formation of nuclei with extra fragments as a result of non-disjunction offer cytological evidence of a means for their increase. Pollen grains with fragments are no doubt functional at least occasionally, if we may extrapolate from the results of Kayano (1956), who found almost a 1:1 ratio of $2n:2n+f$ plants in the cross *Lilium callosum* $2n \text{ ♀} \times 2n+f \text{ ♂}$. In this case the fragment appears to be a telocentric from an originally acrocentric supernumerary. As in *F. biflora*, however, no pairing of the fragment with the basic set occurred at metaphase I, though several fragments could pair among themselves.

The western American species *F. lanceolata*, *F. pudica*, *F. recurva* and *F. folcata* are reported to have fragment chromosomes (Beetle, 1944; La Cour, 1951). In addition, Darlington and Wylie (1955) list several Old World species, and also the Californian species *F. pluriflora*, as having B chromosomes; these may be the same type as those present in *F. biflora*. It is possible that such chromosomes are present throughout the genus, in some species frequent, in others rarer. What their role may be in the population dynamics and evolution of the species remains to be determined.

ISOMERIS ARBOREA. This plant has enjoyed a measure of fame since Billings (1937) reported it to be haploid with a highly anomalous embryology. Since then several workers have reinvestigated the embryology and found it to be essentially normal, although with certain peculiar features (Maheswari and Kahn, 1953; Sachar, 1956). The chromosome situation, however, has not yet been clarified. Observations of meiosis made by Mr. Peter Raven of a plant growing near Whitewater, Riverside County, and by the author of one plant from Point Dume, Los Angeles County, and of another from Red Rock Canyon, Kern County, have shown the species to be a diploid with 20 pairs of chromosomes (fig. 2). The chromosomes are small and difficult to stain well, and buds in meiosis are found rather infrequently, so that it is not favorable material cytologically. However, these observations have shown a normal meiotic sequence from diakinesis through telophase II. Further, my examination of pachytene showed two paired strands in clear cells, and in a few instances where the synapsed chromosomes were more widely separated than usual they could be seen to have a similar chromomere pattern. From the figures published by Billings, it seems clear he observed normal meta-



FIGS. 1-6. Chromosome plates. 1, *Fritillaria biflora*: 12 bivalents plus 2 "fragment-pairs"; 2, *Isomeris arborea*: 20 bivalents; 3, *Lupinus superbus* var. *elongatus*: 24 bivalents, the largest with unequal arms; 4, *Lupinus superbus* var. *elongatus*: left, five A bivalents at metaphase or early anaphase, right, five A bivalents at anaphase; 5, *Datura meteloides*: 10 bivalents plus a chain of 4 chromosomes; 6, *Senecio Fremonii* var. *occidentalis*: 20 bivalents plus 1 fragment.

(Fig. 1, $\times 358$; Fig. 2, $\times 952$; Figs. 3-6, $\times 1071$.)

phases and anaphases in both of the meiotic divisions, but as he was convinced that only univalents were present at diakinesis, he interpreted these as equational separations of univalents.

Isomeris arborea must therefore be returned to the category of rather ordinary plants.

LUPINUS SUPERBUS var. *ELONGATUS*. At metaphase 24 bivalents are present. One of them is conspicuously larger than the rest, and I designate it the A bivalent (fig. 3). In the pollen mother cells from one inflorescence this bivalent was unequal, that is, one chromosome was shorter than the other. Judging from metaphase appearances the A chromosomes are probably acrocentric, and regularly form a chiasma in the short arm. In about ten to twenty per cent of the cells the longer (unequal) arms also show evidence of a chiasma. Figure 4, right, shows the appearance of 5 A bivalents with a chiasma in the short arm; figure 4, left, 5 with chiasmata in both arms. It is possible that the A chromosomes usually form a chiasma in each arm, and that early terminalization in the longer arms releases them from their association. This is suggested by the fact that clear one-chiasma bivalents appear further along in anaphase separation than those with two chiasmata.

White (1954) has given a diagram showing the various types of meiotic segregations which have been observed or are presumed to occur with unequal bivalents of orthopteroid insects. The segregation at the first division will depend upon three factors: the position of the centromere, the position of the chiasmata, and the position of the inequalities. His diagram is based on two assumptions: that the extra segment is terminal rather than interstitial, and that only one chiasma is formed in the unequal bivalents. White has based these two assumptions on the evidence presently available from grasshoppers and phasmids. In *Lupinus superbus* we have what appears to be an example of an interstitial inequality in an unequal bivalent where chiasmata are formed in each arm, a situation for which White had no examples. The evidence for the existence of more than one chiasma in the A bivalent is unequivocal: two-chiasmata bivalents have been seen in many metaphase cells. The evidence for the interstitial position of the inequality is less direct. It depends on the fact that only reductional separations of the inequality have been observed in both one-chiasma and two-chiasmata A bivalents. Should a chiasma be formed in the long arm proximal to a terminal inequality, then an equational separation would result, with one chromatid of the anaphase chromosome longer than the other. Such equational separations were never observed in about fifty cells analyzed, although it must be admitted that equational separations might not be readily detected, since the chromosomes are rather small. Furthermore, only terminal junctions have been found in the unequal arm of the A bivalent at metaphase, while a chiasma proximal to an inequality would be expected to remain interstitial at this stage. It thus appears that reductional separation of the inequality is the rule, and hence that it occupies an interstitial position in the chromosome arm. Whether it is a duplication, a deficiency, or a heterochromatic region (as is so often the case in insects), has not been determined.

Two other chromosomal types might be expected in the population, namely the corresponding homozygotes. The size difference between the A chromosomes is great enough so that there should be no difficulty dis-

tinguishing them. First metaphase was studied in another inflorescence (and hence probably from another plant). In this case both members of the A bivalent appeared about the same size, and were as large as the larger member of the heterozygous plant. If the inequality is a deficiency, the homozygote for the smaller member may not be viable. A much larger sample of the population would be desirable in order to determine the prevalence of the three types, and to compare their frequencies with the expectation based on the Hardy-Weinberg formula.

OENOTHERA CALIFORNICA var. *CALIFORNICA*. The plant examined of this collection was a tetraploid ($n=14$). A varying number of pairs and rings of four chromosomes was found at diakinesis and metaphase, the maximum seen being six rings of 4 plus 2 pairs. The pairing observed suggests that this species was derived from a diploid form which formed 7 bivalents. In *Oe. californica* var. *glabrata*, Lewis et al. (1958) reported two associations of 8 chromosomes, indicative that the diploid form might have been a structural heterozygote. These observations on *Oe. californica* (subgenus *Anogra*) parallel those of Hagen (1950) on two tetraploid species of the subgenus *Raimannia*, who found only pairs or rings of 4 in *Oe. tetragona*, but long chains (of up to 14 chromosomes) and univalents in *Oe. speciosa* var. *Childsii*. In this latter species, diploids are known which form one or two rings of 4, or 7 bivalents.

As is usual with multivalent configurations in the Onagraceae, adjacent chromosomes were regularly segregated to opposite poles at anaphase, thus supporting Garber's (1954) suggestion that if a diploid species shows directed segregation of chromosomes from interchange configurations, the autotetraploid will likewise show directed segregations of the quadrivalents. These observations coincide with those of Catcheside (personal communication to Garber, l.c.) that "*Oenothera* tetraploids from structurally homozygous diploids show almost regularly zigzag orientation of the rings of four." As a consequence of such regular segregation and the lack of lagging chromosomes, fertility in this tetraploid should be quite high.

DATURA METELOIDES. Ten wild plants of this species have been examined and five have been found to be heterozygous for a reciprocal translocation (table 2). A sixth (from Caliente Creek) suggests by frequent univalent formation that it may also be heterozygous for a structural change which is unidentified at present. The plants are apparently not all heterozygous for the same interchange, because a plant from Isabella Reservoir and plants from Putah Creek (*Snow* 322-5, 324-5) characteristically formed rings of four at metaphase, while in the Yucaipa plant (11076B) only chains of four were observed. In a third Putah Creek plant (*Snow* 322-1) variable configurations were formed at metaphase. Usually the groups of four chromosomes appeared as a branched chain (fig. 5). Sometimes one of the pairs of chromosomes of the configuration had a chiasma in each arm, so that the association resembled a kite with the

TABLE 2. LOCALITIES AND METAPHASE ASSOCIATIONS OBSERVED IN WILD INDIVIDUALS OF *DATURA METELOIDES*

LOCALITY AND COLLECTOR	METAPHASE ASSOCIATIONS
Near Ensenada, Baja California, Mexico, <i>Snow</i> (no specimen).	12 (2)
Near Yucaipa, Riverside County, <i>Raven</i> and <i>Snow</i> 11076A.	12 (2)
Near Yucaipa, Riverside County, <i>Raven</i> and <i>Snow</i> 11076B.	10(2) + (4c)
Caliente Creek, Kern County, <i>Snow</i> 248.	12 (2) or 11(2) + 2(1)
Isabella Reservoir, Kern County, <i>Snow</i> 253. (coll. 6/18/54).	10(2) + (4r)
Isabella Reservoir, Kern County, <i>Snow</i> 253A. (coll. 7/30/57).	12 (2)
Putah Creek, south of Davis, Yolo County, <i>Snow</i> 322-1.	10(2) + (4c) or 10(2) + (4r)
Putah Creek, south of Davis, Yolo County, <i>Snow</i> 322-5.	10(2) + (4r)
Putah Creek, south of Davis, Yolo County, <i>Snow</i> 322-8.	12 (2)
Putah Creek, west of Davis, Yolo County, <i>Snow</i> 324-5.	10(2) + (4r)

(2) = bivalent

(1) = univalent

(4c) = chain of four

(4r) = ring of four

tail coming off one side. Other configurations observed, much less frequently, were a "T" with a univalent, a non-disjunctional ring of 4, and 12 bivalents.

Staiger (1955) has found interchanges in natural populations of the mollusc *Purpura lapillus* which lead to metaphase configurations similar to those which I have found in one plant (*Snow* 322-1). He has shown how they may be accounted for by the interchange of short end pieces of metacentric chromosomes plus variations in chiasma formation. The same scheme can account for the configurations in this plant of *Datura meteloides*. The translocations in other plants probably represent larger exchanges of chromosome end segments.

Four chromosomal arrangements have been found in this species by Satina (1953), and one of them (type I) has been compared to the standard race of *Datura stramonium*. The other three arrangements presumably differ from type I by reciprocal translocations. The type I arrangement has been found in twenty-eight races. Unfortunately the origin of none of these races is cited in the paper, so that the geographical distribution of this type is unknown. Furthermore, the existence in nature of individuals heterozygous for reciprocal translocations was not reported for *D. meteloides*, and apparently has not been for any other species of *Datura*, even though individuals of the same species may be homozygous for different chromosome arrangements while members of different species invariably are.

Study of *D. meteloides* is being continued with the view of discovering the role translocations may play in the populations.

SENECIO FREMONTII var. *occidentalis*. The extra chromosome in this

material is a small fragment about one-fourth the length of an arm of the longer chromosomes of the complement at diakinesis. At this stage it is often found lying in the proximity of a bivalent with widely diverging arms, one of which appears shorter than the other by about the size of the fragment. The fragment may even appear attached to this arm by strands of stainable material. With about an equal frequency, however, it is found completely free of this readily-recognizable bivalent (fig. 6).

Stages later than diakinesis were not favorable for study in these preparations. In a few metaphase cells which could be analyzed, the fragment was attached to a bivalent, probably a continuation of a diakinetid association which was so often observed. The fragment was included in one of the daughter nuclei in all instances save one. In this one instance, out of about fifty cells in telophase examined, the fragment had been excluded and was dividing.

Department of Genetics,
University of California, Davis

LITERATURE CITED

- BEETLE, D. E. 1944. A monograph of the North American species of *Fritillaria*. *Madroño* 7:133-159.
- BILLINGS, F. H. 1937. Some new features in the reproductive cytology of Angiosperms, illustrated by *Isomeris arborea*. *New Phytol.* 36:301-326.
- BRADLEY, M. V. 1948. A method for making aceto-carmin slides permanent without removal of the cover slip. *Stain Tech.* 23:41-44.
- CLELAND, R. E. (ed.) 1950. Studies in *Oenothera* cytogenetics and phylogeny. Indiana Univ. Publ. Sci. Ser. No. 16. 348 pp.
- DARLINGTON, C. D. 1939. Misdivision and the genetics of the centromere. *Jour. Genet.* 37:341-364.
- . 1940. The origin of iso-chromosomes. *Jour. Genet.* 39:351-361.
- and A. P. Wylie. 1955. *Chromosome Atlas of Flowering Plants*. George Allen and Unwin, Ltd. London.
- GARBER, E. D. 1954. Cytotaxonomic studies in the genus *Sorghum*. III. The polyploid species of the subgenera *Parasorghum* and *Stiposorghum*. *Bot. Gaz.* 115:336-342.
- HAGEN, C. W., JR. 1950. A contribution to the cytogenetics of the genus *Oenothera* with special reference to certain forms from South America, in Cleland, 1950, pp. 305-348.
- KAYANO, H. 1956. Cytogenetic studies in *Lilium callosum*. II. Preferential segregation of a supernumerary chromosome. *Mem. Fac. Sci., Kyushu Univ., Ser. E*, 2:53-60.
- LA COUR, L. F. 1951. Heterochromatin and the organization of nucleoli in plants. *Heredity* 5:37-50.
- LEWIS, H., P. H. RAVEN, C. S. VENKATESH, and H. L. WEDBERG. 1958. Observations of meiotic chromosomes in the *Onagraceae*. *El Aliso* 4:73-86.
- MAHESHWARI, P. and R. KAHN. 1953. Development of the embryo sac, endosperm, and embryo in *Isomeris arborea*—a reinvestigation. *Phytomorphology* 3:446-459.
- SACHAR, R. C. 1956. The embryology of *Isomeris*—a reinvestigation. *Phytomorphology* 6:346-363.
- SATINA, S. 1953. Chromosome end arrangements in *Datura innoxia*, *D. meteloides*, and *D. metel*. *Am. Jour. Bot.* 40:638-646.
- STAIGER, H. 1955. Reziproke translokationen in natürlichen populationen von *Purpurella lapillus* (*Prosobranchia*). *Chromosoma* 7:181-197.
- WHITE, M. J. D. 1954. *Animal Cytology and Evolution*. 2nd edition. Cambridge University Press.

CHROMOSOME COUNTS IN THE GENUS *GAYOPHYTUM*¹

DAVID G. DIXON

Gayophytum, an annual member of the family Onagraceae, consists of sixteen recognized taxa grouped into eight species. The genus, founded in 1832 by A. de Jussieu on a South American plant, *Gayophytum humile* Juss., is confined to narrow ecological niches along the cordillera of North and South America from Canada to Cape Horn, with an interval in Mexico and Central America where it has not been reported. It has not been found outside the mountain ranges of the western Americas.

As a genus, *Gayophytum* is very poorly known owing to the small size of the plants, the insignificant flowers (rarely as large as 5 mm. across), and the relative difficulty of obtaining specimens. The plants have linear-ob lanceolate leaves and very slender, diffusely branched stems. The ultimate branchlets are often filiform and bear numerous tiny four-petaled flowers in the upper axils. The bushy habit of the plants often with a great number of branching thread-like stems gives them a fuliginous aspect, and when in flower, the blossoms appear to be floating near the ground, hence the popular common name "Ground Smoke."

The flowers are perfect, actinomorphic and tetramerous. The sepals are in the orthogonal and the petals in the diagonal planes. Ovaries are bicellular and inferior, with ovules in one row in each loculus. The fruit is dry, splitting loculicidally and septifragally so the inner portion of the fertile carpels is left as a seed-bearing column in the center (Saunders 1940).

Gayophytum may be distinguished from the very similar *Epilobium* by the lack of coma on the seeds, by the two-celled ovaries and fruits, and by having solitary pollen grains.

Plants of *Oenothera* of similar size and habit and with equally reflexed sepals may be distinguished from *Gayophytum* by their more elongate hypanthium and four-celled ovary. The prevailing flower color of *Oenothera* is yellow; the flowers of *Gayophytum* are white, turning rose-purple with age.

In the words of Munz (1932): "The genus *Gayophytum* offers an unusually interesting series of plants varying in a comparatively small number of characters, and these in every conceivable combination. Flowers may be small or large; capsules may be sessile or pedicelled, erect or spreading-deflexed, short or long, torulose or not torulose; the minute hairs may be appressed or spreading; seeds may be glabrous or pubescent; branching may be basal or distinctly above the base. The attempt at classification . . . may be quite artificial; it has been arrived at only after

¹ A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Botany at the State College of Washington, 1957. The author wishes to express his appreciation to Dr. Adolph Hecht who suggested the problem, and served as advisor during the course of the research, and to Dr. Marion Ownbey who provided many suggestions during the preparation of the manuscript.

TABLE 1. CHROMOSOME NUMBER AND SOURCE OF GAYOPHYTUM COLLECTIONS STUDIED

SPECIES	CHROMOSOME No. 2n	SOURCE
<i>G. Helleri</i> var. <i>glabrum</i> Munz	14	Washington, Douglas Co.: 6 mi. N. of Withrow, Route 10-B, on <i>Artemisia</i> knolls, <i>Dixon 9</i> .
<i>G. humile</i> Juss.	14	California, Mono Co.: Carnegie Inst. Timberline Station, Slate Creek Valley, 10,000 ft. elev. <i>H. Lewis</i> .
<i>G. lasiospermum</i> Greene	28	Idaho, Valley Co.: 1 mi. S. of Lake Fork, Route 15, on coarse gravel of ditches, <i>Dixon 14</i> .
<i>G. lasiospermum</i> Greene	28	Idaho, Adams Co.: 4.5 mi. S. of New Meadows, on cut-over <i>Pinus ponderosa</i> flat, W of Route 95, <i>Dixon 17</i> .
<i>G. Nuttallii</i> T. & G.	28	Washington, Okanogan Co.: 5 mi. W. of Republic Route 4, on moist clay and gravel road-cut, <i>Dixon 7</i> .
<i>G. Nuttallii</i> T. & G.	28	Idaho, Valley Co.: within city limits of McCall, on sand banks, <i>Dixon 12</i> .
<i>G. Nuttallii</i> T. & G.	28	Idaho, Latah Co.: on roadside sand of Saddle between Twin Buttes, Moscow Mountain, <i>Rumely & Dixon</i> .
<i>G. Nuttallii</i> T. & G.	28	California, Tuolumne Co.: 4.4 mi. W. of Kennedy Meadows, Highway 108, Deadman Creek at 6,000 ft. elevation. <i>Balls & Everett 18074</i> .
<i>G. Nuttallii</i> var. <i>Abramsii</i> Munz	28	Washington, Stevens Co.: 2 mi. S. of Kettle Falls, Route 22, fine sand in <i>Pinus</i> flat, <i>Dixon 3</i> .
<i>G. racemosum</i> var. <i>erosulatum</i> Munz	28	Idaho, Valley Co.: 1 mi. S. of Lake Fork, Route 15, on coarse gravel road-bank, <i>Dixon 15</i> .

much study. Unfortunately geographical distribution which is so often a great aid to the systematist, is not very useful here, and one almost doubts the validity of some of the entities maintained because of lack of continuous or definite distribution. Furthermore, the floral parts are so minute that individual specimens can easily be thrown into the wrong group. Yet, as I have worked over many hundreds of sheets at various times . . . , I have been forced to conclude that there are several very real and definite entities in the genus."

The taxonomic treatments of Trelease (1893) and Munz (1932, 1951, 1952) have proved satisfactory and have been followed in this study. Trelease expressed the opinion that *Gayophytum* may be of rather recent

differentiation from *Oenothera*, representing an accentuated montane-type.

A possible origin of *Epilobium* ($n=18$) by the "addition" of eleven chromosomes of *Gayophytum ramosissimum* T.&G. ($n=11$) to the seven of *Boisduvalia* ($n=7$) has been suggested by Johansen (1933). This view that *Epilobium* may be of hybrid origin, however, has not been supported.

Very little is known about the cytology of *Gayophytum*. Johansen's (1933) work on *G. ramosissimum* is the only published report of previous cytological study in this genus. It was with the objective of adding to the cytological information on this genus that the present study was undertaken.

Plants for this study were collected during the late summer months of 1955 and 1956, in eastern Washington, central and southwestern Idaho, and northeastern Oregon. Additional seeds were supplied by Dr. Harlan Lewis and by Dr. P. A. Munz. Dr. Munz kindly identified the plants used.

Plants of *Gayophytum nuttallii* T.&G. were grown to maturity in the greenhouse, but no other species survived past the seedling stage in cultivation. Root-tips were the source of the meristematic tissues used in this study.

Field collected root-tips were fixed in Belling's metaphase modification of Navashin's fixative. Paraffin sections cut at ten microns were prepared and then stained by the crystal violet-iodine method (Johansen, 1940).

Chromosome numbers of $2n=14$ and $2n=28$ were found in the plants studied. Johansen (1933) lists the number $2n=22$ for the North American species, *Gayophytum ramosissimum*. The number $2n=28$ was found to be constant in collections of *Gayophytum lasiospermum* Greene, *G. Nuttallii*, *G. Nuttallii* var. *Abramsii* Munz, and *G. racemosum* var. *erosulatum* Munz. The number $2n=14$ was discovered in *Gayophytum Helleri* var. *glabrum* Munz and in *G. humile*.

On moistened filter-paper in Petri dishes kept at room temperature, seeds of the 14-chromosome species had a relatively vigorous germination percentage of 11 per cent, whereas those of the 28-chromosome species under the same conditions may have as low as one-fourth of 1 per cent germination.

The two 14-chromosome species were collected at elevations of 2,000 and 10,000 feet, respectively. The 28-chromosome species are from elevations ranging from 900 feet to over 6,000 feet. The 14-chromosome species tend to be smaller in stature and have smaller flowers than those with 28 chromosomes, but marked phenotypic differences are not evident between the two groups.

DISCUSSION

It is suggested that the 14 chromosomes counted in *Gayophytum Helleri* var. *glabrum* and in *G. humile* may make up the basic diploid complement of the genus. If this is the case, it may be assumed that the species with 28 chromosomes constitute a number of tetraploid taxa. The chromo-

somes do appear in reasonably recognizable sets of four in these species.

The chromosome numbers reported in this root-tip study are not consistent with the 22 chromosomes reported for *Gayophytum ramosissimum* (Johansen, 1933) in which embryo-sac meiosis was examined. The species previously studied was not available for examination in the current investigation. The possibility exists of an aneuploid series of chromosomes in *Gayophytum*. The count of 22 might be an instance of a hyperploid ($3x + 1$) constitution.

A brief survey of the chromosome numbers (Darlington and Wylie, 1956) in the family Onagraceae reveals a range of basic numbers occurring in *Clarkia* (including *Godetia*) ranging from $x = 5$ through 7, 8, and 9; *Gaura* may have $x = 7$ or 9. Other genera reported show $x = 7$ constant for *Oenothera*, $x = 8$ for *Jussieuia*, $x = 11$ for *Circaea*, *Lopezia*, and *Fuchsia*, with $x = 15$ for *Zauschneria* and $x = 18$ for *Epilobium*.

It is apparent that *Gayophytum* fits most closely into the chromosome series of the family near *Oenothera*. Such a position would agree with Trelease's view (1893) that *Gayophytum* may be of rather recent differentiation from *Oenothera*.

SUMMARY

Mitotic chromosome studies were made on ten collections of six taxa representing five species of *Gayophytum*. Chromosome numbers of $2n = 14$ and 28 were found. The numbers 14 and 28 are in addition to the one of 22 previously reported for the genus.

Chromosome counts for *Gayophytum Helleri* var. *glabrum*, *G. humile*, *G. lasiospermum*, *G. Nuttallii*, *G. Nuttallii* var. *Abramsii*, and *G. racemosum* var. *erosulatum* are reported for the first time. Voucher specimens are on file in the herbarium of the State College of Washington.

Department of Floriculture and Ornamental Horticulture,
University of California, Los Angeles 24, California.

LITERATURE CITED

- DARLINGTON, C. D. and WYLIE, A. P. 1956. Chromosome atlas of flowering plants. Macmillan Company. New York.
- JOHANSEN, D. A. 1933. Studies on the morphology of the Onagraceae VII. *Gayophytum ramosissimum*. Bull. Torrey Club 60:1-8.
- . 1940. Plant microtechnique. McGraw-Hill Book Co. New York and London.
- MUNZ, P. A. 1932. Studies in Onagraceae VIII. The subgenera Hartmannia and Gauropsis of the genus *Oenothera*. The genus *Gayophytum*. Am. Jour. Bot. 19: 755-778.
- . 1951. *Gayophytum*, in Abrams, L., Illustrated flora of the Pacific states, Vol. 3. Stanford University Press, Stanford, Calif.
- . 1952. *Gayophytum*, in Davis, R. J., Flora of Idaho, William C. Brown. Dubuque, Iowa.
- SAUNDERS, E. R. 1940. Floral Morphology. Chem. Publ. Co. New York.
- TRELEASE, A. 1893. Revision of the North American species of *Gayophytum* and *Boisduvalia*. Ann. Rep. of the Mo. Bot. Gard. 5:107-122.

REVIEWS

Spring Flowers of the Lower Columbia Valley. By CLARA CHAPMAN HILL. Illustrated by Mary Comber Miles. pp. xi + 164. University of Washington Press. 1958. \$3.00.

Certainly one of the most frustrating and interest-stifling experiences of a novice at plant identification is his attempt to name a plant by using the formidable terminology of the keys and descriptions of technical manuals. *Spring Flowers of the Lower Columbia Valley* is the newest of a small number of "easy" manuals which have been designed to accustom the beginner to this terminology and to the technique of using the more detailed and comprehensive manuals of the Pacific Northwest flora.

This small book is not, as its title suggests, a manual of the vernal flora of the lower Columbia River valley. Rather it is a florula of what might more appropriately be called the lower Willamette River valley in the vicinity of Portland, Oregon. It describes, in a simplified manner, about 200 of the more conspicuous herbs and shrubs of the season in that region. Use of technical words in the keys and descriptions is held to a minimum; a number of these terms are introduced by means of illustrative line drawings. Additional terms can be found in the glossary which, however, offers some definitions so oversimplified as to be quite uninformative. Approximately one-third of the species treated are adventive. Unfortunately no trees or ferns are considered, even though these groups often attract much attention from the beginners for whom this book was written. Following the introduction is a key to the genera; in the text the species are arranged under family headings and in some instances there are keys to the species within genera. The text is enlivened by brief but interesting notes on the natural history, uses, and lore of various species. Some of the families are characterized by short descriptions, a few of which are so truncated that they do not adequately distinguish one family from another. For example, the traits of the Saxifragaceae as stated could apply equally to the Crassulaceae for which no diagnosis is given. A problem common to all books which cover only a segment of a flora is the chance of misidentification by a beginner of a plant which appears to "key out" correctly, but is in fact unlisted in the book. Nevertheless, the selection of species considered is good, and few errors should arise providing it is used in the season and the region it is intended to cover.

The format, binding, and price are attractive; the nomenclature is up-to-date and the book seems virtually free of typographical errors. For summer and autumn work its owners should feel confident and experienced enough to graduate to other more technical manuals of broader scope, many of which are listed in a bibliography. However, even after they have gone on to other works, they will want to keep this book on the shelf for the occasional pleasure of leafing through it to savour the 71 superb, full-page line drawings by Mary Comber Miles. Perhaps these are its greatest recommendation.—ROBERT ORNDUFF, Department of Botany, University of California, Berkeley.

Spring Flora of the Dallas-Fort Worth Area [,] Texas. By LLOYD H. SHINNERS. v, 514 pp., 11 plates, 2 maps. Published by the author, Southern Methodist University, Box 473, Dallas 5, Texas. 1958. \$4.75 (by mail, \$4.85).

The author of this unusual book has been working since 1945 in an area for which there has never been a complete descriptive flora. It is a particularly interesting area because it centers about the Blackland Prairie which supports a large endemic and near-endemic flora, and because the tension zones lying east and west of the prairies here are complicated and have been little known in detail. The author's apology explains a little of why this is still not a complete flora; this is worth quoting in some detail because it helps to point up one of the most unusual features of the book, namely the extent to which it is truly a production of the author's own work and thought:

"Spring Floras are a peculiarly American institution. In almost any other country one would get a complete flora, not just a sample. I do not know for certain all the reasons for this, but most are not scientific. Expediency, laziness, indifference, incompetence, and imitativeness are all involved, along with distractions, lack of facilities and time, and the difficulties involved in writing a complete work in most parts of the country—which itself has never had a whole flora completed for it. This book is largely an abstract of my *Flora of North Central Texas*, which after thirteen years' labor is still unfinished. A major part of the delay is due to the fact that I have had during the same time to create the elaborate facilities needed to produce such a work. Some has been due to my conceit in determining at the start that everything would be written by myself, and based on live plants and specimens. Nothing was to be farmed out to specialists; only the absolutely unavoidable minimum would be taken from publications."

A little further along Dr. Shinnars hints at the real justification for a Spring Flora; in his part of Texas the early spring is the only major season of bloom. The growing season may begin in January and reach a climax in February or early March; before the beginning of May the hot season has set in and everywhere the sun-dried skeletons of plants proclaim the onset of summer.

The book was written to be used. The keys avoid the use of obscure characters, and the terms used in them are simple and clear. In the descriptions an attempt has been made to combine brevity with emphasis on diagnostic features. A useful feature is the inclusion of common spring-flowering cultivated plants likely to be encountered in the area.

The author warns the reader, however, that he has not prostituted science for the sake of popularity:

"There is no magic which will make it child's play to find out the names of so huge a quantity of variable plants. No real familiarity with them can be acquired without using technical terms. No worthwhile list of them is possible without using scientific names. If you wish something painless and effortless, the pursuit of botany is not for you. Nature gives away few secrets to the lazy, and none to the incompetent".

The total number of species considered in the Flora is about 1650, including three that are described for the first time. The largest families, not surprisingly, are the Compositae, Gramineae and Leguminosae. The key to families, if it works, will be a joy to the earnest student who has so often been frightened away from regional floras by keys that are replete with references to details of ovule structure, placentation and the like. Dr. Shinnars' key, appropriately enough in a Spring Flora, is based entirely upon floral characters and vegetative characters. Some technically minded botanists may shudder at having *Galium*, Orchidaceae, *Lonicera japonica* and *Arisaema* associated in the key under the heading of HERBACEOUS DICOTS. I found it hard to use this part of the key. In numerous other trials in other parts of the key I found family after family readily identifiable.

The keys to genera represent something of an achievement, especially in the families like Cruciferae, Leguminosae, Umbelliferae and Compositae where generic differentiations have heretofore been based almost entirely on characters of the fruits. Other authors, of course, have attempted, like Shinnars, to construct generic keys using floral characters only. The late Norman C. Fassett did this with signal success in the *Spring Flora of Wisconsin*. Fassett was dealing with 15 genera of Leguminosae; Shinnars treats 48. Fassett had 13 genera of Compositae; Shinnars keys out 64 genera without mentioning the mature achenes. Specialists may pick flaws in the treatments of their favorite groups, but it seems to me this is a praiseworthy attempt to focus attention upon floral characters that have usually been overlooked by botanists.

The author's concepts of families and genera are for the most part broad ones.

He makes of Leguminosae a single family, and Rosaceae another. His treatment of the Liliaceae-Amaryllidaceae group, although not out of line with modern thought, is not conservative. Perhaps his most startling departure from general practice is in the recognition of *Chamaesyce* as distinct from the rest of Euphorbia. His concept of the species (based primarily on consideration of morphology and geographic area, as he says on page 469) is a rather inclusive one that in general seems appropriate in the flora with which he is dealing. In *Crataegus*, for example, Shinnery recognizes 14 species, relegating to synonymy (sometimes with a question) approximately as many additional species described by earlier authors. In *Rubus* Shinnery recognizes 5 native species, listing in synonymy 12 additional species described by Bailey.

Throughout the book an appeal is made to the common-sense of the reader. Manufactured "common names" are avoided and indeed anathematized. Comments on exceptional nomenclatural situations, taxonomic oddities or complexities, and extraordinary or unusual features of the plants themselves, are frequently mentioned. Nomenclatural synonyms are included sparingly, chiefly for the sake of clarity when there have been recent changes in the application of names.

Following the formal systematic treatment of the flora, Dr. Shinnery has included a series of plates illustrative of certain plant families, and finally a series of appendices explaining technical terms, the use of keys, the justification for a standard system of plant-nomenclature, and the preparation of herbarium specimens. There is a glossary and a short discussion of ecology, vegetational types and the botanical history of the region.

In general this is a very commendable book that will command a great deal of respect from amateur and professional botanists alike. It should be particularly effective as an introduction to Botany when used by the student, in or out of school, who is initially attracted by a flowering plant and wants to learn more about its identity and its characteristics. As a contribution to floristics the book is patently an introduction to the author's projected and much larger work. In its present form, hastily gotten out with a regrettably large number of typographical errors, it must be nevertheless regarded as a remarkably good and scholarly flora of an area where such a work was urgently needed. The book begins with a quotation from Gerard's *Herball* of 1597, and this review may well close with a line from the Book of Daniel, long ago quoted by Olof Swartz in expressing his appreciation to those who contribute to floristic knowledge: *Plurimi pertransibunt et multiplex erit scientia.*—ROGERS McVAUGH, University of Michigan, Ann Arbor.

NOTES AND NEWS

ALLIARIA OFFICINALIS ANDRZ. IN OREGON.—In the spring of 1959 a cruciferous plant which could not be identified in the regional manuals was collected in an undisturbed forested portion of the Reed College campus in southeastern Portland, Oregon (Ornduff 5057). This plant has proved to be the European garlic-mustard, *Alliaria officinalis* Andr., which has not previously been reported from the Pacific states. The Reed College colony of this biennial species was composed of about two dozen freely seeding plants. It had not been recorded in a thorough, unpublished census of the campus flora made in 1938. Subsequently a second colony of about the same size was located in a wooded tract in southwestern Portland. This species is well established and widespread in eastern North America and appears well on its way to becoming a permanent member of the adventive flora of at least the Portland area as well.—ROBERT ORNDUFF, Department of Botany, University of California, Berkeley.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers,	
Volumes 1 and 250
Succeeding numbers,	
(except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$4.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary

Department of Botany

University of California, Berkeley 4, California



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 4

OCTOBER, 1959

Contents

	PAGE
THE GRASS GENERA <i>ORCUTTIA</i> AND <i>NEOSTAFFIA</i> : A STUDY IN HABITAT AND MORPHOLOGICAL SPECIAL- IZATION, <i>Beecher Crampton</i>	97-110
THE TAXONOMIC RELATIONSHIP BETWEEN <i>PICEA</i> <i>GLAUCA</i> (MOENCH) VOSS AND <i>P. ENGELMANNII</i> PARRY, <i>T. M. C. Taylor</i>	111
FIELD STUDIES OF NATURAL HYBRIDIZATION IN THE OREGON SPECIES OF <i>IRIS</i> L. SUBSECTION <i>CALIFOR-</i> <i>NICAE</i> DIELS, <i>Quentin D. Clarkson</i>	115
VARIATION PATTERNS IN FOUR CLONES OF <i>MERTEN-</i> <i>SIA CILIATA</i> , <i>Jeanette S. Pelton</i>	123
NEW COMBINATIONS IN <i>ASTER</i> , <i>Roxana S. Ferris</i>	128
NOTES AND NEWS	128

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

- HERBERT L. MASON, University of California, Berkeley, Chairman
EDGAR ANDERSON, Missouri Botanical Garden, St. Louis
LYMAN BENSON, Pomona College, Claremont, California.
HERBERT F. COPELAND, Sacramento College, Sacramento, California.
JOHN F. DAVIDSON, University of Nebraska, Lincoln.
IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.
MILDRED E. MATHIAS, University of California, Los Angeles 24.
MARION OWNBEY, State College of Washington, Pullman.
IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER
Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—WINSLOW R. BRIGGS.
Department of Biology, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: James R. Sweeney, San Francisco State College, San Francisco, California. First Vice-president: Baki Kasapligil, Mills College, Oakland, California. Second Vice-president: Henry J. Thompson, Department of Botany, University of California, Los Angeles, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: Winslow R. Briggs, Department of Biology, Stanford University, Stanford, California.

THE GRASS GENERA ORCUTTIA AND NEOSTAPFIA: A STUDY IN HABITAT AND MORPHOLOGICAL SPECIALIZATION

BEECHER CRAMPTON

Without a doubt, the endemic genera *Orcuttia* and *Neostapfia* are the most unusual and rarest of the California grasses. *Orcuttia* comprises five species and two varieties, while *Neostapfia* is monotypic. All are narrowly restricted annuals which develop in the summer beds of vernal pools and exhibit peculiar morphological features. Their relationship to other grasses is not apparent and quite likely they represent a relict group, the ancestors of which are unknown. Very few collections of them had been made up to the time Hoover (3) made known the degree of speciation and geographical range of the *Orcuttia* species. A relatively small number of these grasses has been collected since.

In cooperation with the Department of Agronomy, University of California, Davis, and its grass research program, the author was privileged to spend part of the summer of 1958 observing the nature of the habitat and making extensive collections of these fascinating grasses. The results were very gratifying, and the success of this specialized exploration has prompted the author to present his findings and to provide additional information about the habit, habitat, and morphological development of these two unique genera in the California grass flora.

The author is especially grateful for the helpful suggestions and criticisms by Dr. G. L. Stebbins, Department of Genetics, and Dr. Jack Major, Department of Botany, both of the Davis campus, University of California.

I. THE NATURE OF THE HABITAT

While many of the Californian grasses are relatively unspecialized as to habitat, *Orcuttia* and *Neostapfia* are restricted to vernal pools. These basins, sometimes called "hog wallows," are best developed on the rolling plains surrounding the Great Valley of California, and to a lesser extent on the valley floor. Rainwater collects in them and stagnates during the winter and spring, and by late spring or early summer it has completely evaporated. The pools are quite variable in extent or area, depending upon the terrain. Some are small, shallow, or circular to irregular shape, and several meters in diameter. Others may be greatly ramified, with numerous islands, while some are quite large, perhaps 500 meters or more in diameter, being then classed as intermittent lakes.

Upon evaporation, the recession of the water from the margin initiates development of a unique flora on the muddy strand. Some plant species, however, depend upon the standing water for seedling development or renewal of perennial growth. It is not unusual to find mature annuals on the margins of the pools, while very young plants of the same species are in active growth at the edge of the receding water. Such annual plants

MADROÑO, Vol. 15, No. 4, pp. 97-128. October 30, 1959.

as *Allocarya*, *Pogogyne*, *Downingia*, and *Navarretia* often show this pattern and become generally distributed over the beds. The grasses, *Deschampsia danthonioides* and *Hordeum hystris*, are restricted to the margins. Of the perennials, *Eryngium* may be generally distributed or marginal, while *Eleocharis palustris*, *Marsilea*, and sometimes *Damasonium* are in the central or deeper portions of the basins. The distribution or occurrence of any one plant species in this environment is quite dependent upon size, depth, and soil type of the pool and the length of time of standing water.

Orcuttia and *Neostapfia* require a very special type of vernal pool. The concept of "hog-wallow" should be amended to "elephant-wallow" to satisfy the environmental demands of these grasses. Primarily, the optimum size of their vernal basins is about 20–100 meters or more in diameter or length. Secondly, such basins must neither be drained naturally nor artificially, for long periods of standing water are a necessity. Dry, unfavorable years result in a paucity of the grasses, while years of heavy rainfall such as 1958 (Table 1) are responsible for their peak development. The best stands of either *Orcuttia* or *Neostapfia* occur mostly in the absence of other vegetation (fig. 1E). The adobe muds in the large vernal pools, with their barren, dried, cracked, and often well trampled surfaces, are ideal sites. The presence of the ubiquitous vernal pool *Eryngium vaseyi* and the sedge, *Eleocharis palustris*, restricts the density of *Orcuttia* and *Neostapfia*. Any dense stand of either of these perennials has relatively few to none of the annual grasses among them. Barren areas or clearings in *Eleocharis* and thin stands or absence of the *Eryngium* become excellent sites for *Orcuttia* development. *Marsilea* apparently has no deterrent effect on the grasses, as it is a frequent associate of them. Relatively few annuals offer competition to *Orcuttia* or *Neostapfia*, *Boisduvalia* being probably the commonest, with occasionally *Eremocarpus* and certain *Euphorbia* species, but in the main most annuals have dried before maximum development of the grasses occurs.

Recognition of the proper habitat of *Orcuttia* and *Neostapfia* simplifies collection of these unusual grasses. The most numerous, shallow, early drying vernal pools can thus be eliminated as sites for their occurrence, and only the large-type pool, with some barren portions, need be considered.

In the past evolutionary history, *Orcuttia* and *Neostapfia* probably developed as shore or strand grasses on the margin of a sea, such as once covered the present Great Valley area. The conversion of the sea to a land surface involved only minor modification in the character of the habitat so that isolated ponds, developing along the shore of the receding sea, became an eventual refuge for these grasses. Perhaps the greatest change came in elimination of salts, yet *Neostapfia* has been found growing on alkali in Colusa (the type locality) and Solano counties. *Orcuttia mucronata* occurs, as far as is known, only on alkali, but other species of the genus favor nearly neutral or perhaps slightly acid soils. It also became

necessary for the plants to withstand the period of summer dryness as developed in the Great Valley and surrounding areas during the geologic changes.

II. THE AREAS OF COLLECTION

The pioneer work by Hoover (3) established geographical ranges for the species of *Orcuttia* and enabled the present writer to visit several areas of known occurrence of these narrow endemics. Aside from studying habitats and associations, extensive collections were made of all species except *Orcuttia californica*, which occurs only in southern California.

A. THE SAN JOAQUIN VALLEY

1. **Stanislaus County.** The low hill and rolling plain areas bordering the Tuolumne River east of Waterford and Hickman, are especially rich in *Orcuttia* and *Neostapfia*. The topography favors development of the larger-type vernal pool. In this region the upland soils are primarily a reddish loam of the San Joaquin series, while the pool beds are light to dark grey adobe of the Alamo series, well permeated with iron compounds which act as cementing materials. Most of the land is grain-farmed, some exists as dry rangeland, while other areas have been converted to irrigated pasture.

In the grainfields between the southern part of Modesto Lake and State Highway 132, there are seven large vernal pools bordering on Dienstag and Reservoir roads. All but one of these basins had excellent stands of *Neostapfia*, four of them with abundant *Orcuttia pilosa*, and a single one with *Orcuttia californica* var. *inaequalis*. Hoover apparently overlooked this particular area of *Orcuttia* and *Neostapfia* while collecting in 1936–1938. The type locality for his *Orcuttia pilosa* lies five miles farther east, the region, as far as determinable, now being irrigated pasture.

Two vernal basins border Dienstag road, the southern one unequally divided by the gravel roadbed (fig. 1-A). The larger and western section of this latter pool is about 100 meters across at the widest point and nearly 125 meters long. Its basin was entirely covered by a magnificent, dense stand of *Neostapfia* (fig. 1-B). A few scattered clumps of *Eleocharis palustris* and *Sida hederacea* were found along the fence adjacent to the road, otherwise there was pure *Neostapfia*. The green "sheet" of this grass was in marked contrast to the dry barley stubble on the surrounding slopes.

The eastern and smaller portion of this vernal pool is bordered by hilly rangeland. At the lowest point, near the road, there was still some standing water on July 28, 1958 (fig. 1-A). Surrounding the murky water, in a semicircle, was a wide band of barren, dark-grey, well-trampled mud. On the periphery of the mud, a pale green band of *Neostapfia* was developing on the cracking, drying, grey adobe. Several resident dairy heifers were intermittently, but actively grazing the grass!

The second vernal pool along Dienstag road is about 100–125 meters long and perhaps 75 meters wide. The bed was a solid stand of *Neostapfia*

with an abundance of *Orcuttia pilosa* along the margin. This unique pattern invariably occurred whenever the two grasses were associated.

Three vernal pools along and south of Reservoir Road were replete with *Neostapfia* and *Orcuttia pilosa* as the sole or major occupants. One pool, however, contained mostly *Orcuttia californica* var. *inaequalis*, very little *Orcuttia pilosa*, and no *Neostapfia*. Another pool was of unique shape, nearly 150 meters long and about 10 meters wide, its bed a pure, solid stand of *Neostapfia*.

The barley field operations in this area apparently do not affect the successful development of these peculiar grasses in their habitat. Undoubtedly the planting machinery disturbs the vernal pool beds in the fall, yet after that they remain undisturbed until harvest, at which time *Orcuttia* and *Neostapfia* are reaching maximum development.

A large playa, about 150 meters or so in diameter, is situated in a small valley leading out of the hilly country three miles east of Hickman. Though the surrounding areas are grain-farmed, the vegetation of this bed differs considerably from those of the previous area. *Neostapfia* is restricted to small patches, while *Orcuttia californica* var. *inaequalis* is more widely dispersed. Active competition is afforded by *Centromadia fitchii*, *Boisduvalia*, and *Eryngium*, with an abundance of dried *Allo-carya*, *Downingia*, and *Navarretia leucocephala*. The more barren areas on the dried and cracked lead-grey adobe support the best stands of both *Orcuttia* and *Neostapfia*.

An extensive reservoir or permanent lake¹ (fig. 1-C) is located on the Loren Rouse Ranch six to seven miles east of Hickman, along the road to La Grange. *Neostapfia* and *Orcuttia pilosa* occur abundantly along the strand, which is subject to vernal flooding and summer drying. This lake has quite likely been developed from a large vernal playa which originally was populated by these two grasses, since the margins of man-made reservoirs are not ordinarily sites for development of either of these grass genera. If planted, they might very well become adapted to reservoir strands.

Summer fallowing of the hilly grainland to the south had closely approached, nevertheless had not disturbed the strand. Dry rangeland and irrigated pasture surround the lake on the north and east, respectively, though neither operation had disturbed the habitat.

The old Paulsell warehouse is located along the old Sierra railroad northeast of Waterford. The land area is now largely devoted to irrigated pastures except for the hilly, dry rangeland to the north. The distinctive *Orcuttia greenei* was found in a large, undisturbed playa at the southwestern base of a prominent knob-like hill. The playa basin is perhaps 200–250 meters in diameter and composed of black, deeply-cracked adobe. Aside from the dense, dried *Allo-carya* cover, *Eryngium* and *Eremocarpus* were dominant, with some *Eleocharis palustris* and *Boisduvalia*.

¹ Since the above was written, it has been learned that this is a natural pool.

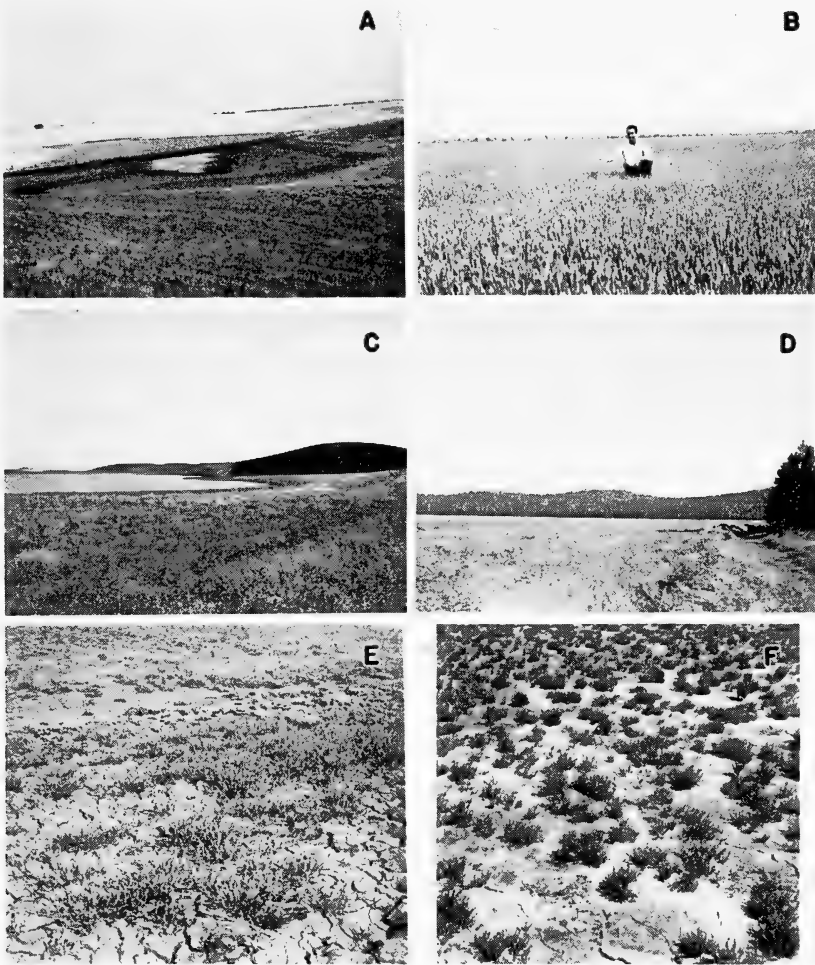


FIG. 1. The habitats of *Orcuttia* and *Neostapfia*. (A) Large vernal pool in the barley-farmed area south of Modesto Lake, east of Waterford, Stanislaus County. Dienstag Road divides the basin. (B) The author in the solid stand of *Neostapfia* present in the far portion of A. (C) Lake on the Rouse Ranch east of Hickman, Stanislaus County, the strand of which has an abundance of *Neostapfia* and *Orcuttia pilosa*. (D) Goose Valley, Shasta County, the type locality of *Orcuttia tenuis*. The author collected the grass in the ditchbed at the right. (E) *Neostapfia* growing on a typical soil of a vernal pool bed. Note the cracks and absence of other vegetation. *Eremocarpus* lines the bed in the background. (F) Habitat of *Orcuttia mucronata*. *Frankenia* and the prostrate *Eryngium aristulatum* are the only associates.

The *Orcuttia* was not abundant, but occurred mostly as scattered plants in areas containing the least *Eryngium* and *Eremocarpus*.

2. Merced County. In the vicinity of the old Ryer station, located 6.5 miles south of Montpelier, there are two large-type vernal pools containing *Orcuttia californica* var. *inaequalis*. The rather uniform rolling hill country in this area is all grain-farmed, with rather numerous, smaller-type vernal pools. The large playa to the west is basically a lead-grey colored adobe, well populated with *Centromadia fitchii*, *Centromadia pungens*, *Sida hederacea*, *Boisduvalia* and marginal *Eryngium* as well as the dried *Allocarya*, *Downingia* and *Navarretia leucocephala*. The *Orcuttia* was most abundant in areas of the least competition.

The eastern vernal pool harbored a dense stand of *Orcuttia californica* var. *inaequalis* to the near exclusion of other plants. Apparently the basin had been completely cultivated during barley planting, for faint furrows were evident over the pool bed. The *Orcuttia* was exceedingly robust, some of the plants being 12–15 cm. high and with as many as 60 culms, a development far in excess of those in the neighboring playa. Aside from dried *Allocarya*, only a few scattered plants of *Centromadia* and *Eremocarpus* were present.

North of Legrand, in typical rolling plain rangeland, is a large playa perhaps 300–350 meters in diameter. The soil of the basin is a black adobe, becoming exceedingly deeply cracked when dry. Some of the cracks extended from three-fourths to nearly a meter in depth and from 5–10 cm. across at their aperture. A dense stand of *Eremocarpus* covered the major portion of the bed, the whole appearing from a distance as a silver-grey “lake.” Large specimens of *Orcuttia greenii* were numerous in areas of the least *Eremocarpus*, though scattered individuals occurred throughout the playa. *Boisduvalia* was perhaps the closest and only other associate.

B. THE SACRAMENTO VALLEY AND NORTHERN CALIFORNIA

1. Solano County. A magnificent alkaline, intermittent lake is situated in a rolling plain area twelve miles south of Dixon, Solano County. It is shallow, has no drainage, and is about 500 meters in diameter. The predominant vegetation in the lake basin is *Frankenia grandifolia*, *Cressa truxillensis*, *Sida hederacea* and *Eryngium aristulatum*, with some patches of *Eleocharis palustris*. The marginal strand is largely *Distichlis*, *Lippia* and *Navarretia bakeri*. The dried crust varies from a uniform, glaring-white pavement to a tan and cracked surface. On the latter type, *Neostapfia* and an undescribed species of *Orcuttia* grew in association with *Frankenia* and *Eryngium* (fig. 1-F). Both grasses, at their best, were rare occupying an exceedingly small area of about 15–20 meters in diameter. The *Orcuttia* will be described later in this paper as *Orcuttia mucronata*, while the occurrence of *Neostapfia* here represents a new area for California.

2. Sacramento County. According to Hoover (3), *Orcuttia californica* var. *viscida* is not known to occur outside of Sacramento County. The Orangevale area now shows a distinct waning of the grass, and in all probability the habitat will be eliminated by residential development.

On the higher, rolling plains north of Sloughhouse, one large vernal pool and several smaller, but deep ones, support fairly good stands of this attractive *Orcuttia* and represent its type locality. It was conspicuous along the margins and in some parts of the bed of the large pool. This greater basin, 100 or more meters in length and with some ramification, is largely a barren and stony bed. The cracked, lead-grey, adobe soil is well supplied with iron concretions, apparently an indication of the type of soil several *Orcuttia* species prefer. Some patches of *Eleocharis palustris* and *Eryngium* were present, but these species were certainly not diffuse in any area of the pool.

3. Butte County. A single vernal pool on the rolling plains about ten miles southeast of Chico was well supplied with *Orcuttia greenei* and probably represents the type locality of this species. The basin, 75–100 meters in diameter, is composed of a grey-black, crumbly, stony, and pebbly soil. Over the major portion of the pool the marginal vegetation of *Eryngium* and *Eremocarpus* gave way to an abundance of the *Orcuttia* and to the prostrate annual *Euphorbia hooveri*.

4. Tehama County. *Orcuttia tenuis* is endemic to northern California, preferring soils probably derived from volcanic substrates. Only certain areas of Tehama, Shasta, and Lake counties have the proper environmental conditions, each of them in entirely different settings.

In Tehama County, on a rocky, volcanic plateau eleven miles northeast of Red Bluff, lies an extensive dry lake known as Hog Lake. The basin is perhaps 300 meters wide and 1500 meters long, surrounded by mixed, open grassland and blueoak woodland. The western shallow portion and the marginal strand were largely populated by *Eryngium*, while the deeper portions contained *Eleocharis palustris* and *Damasonium*. The best development of *Orcuttia tenuis* occurred in the barren, stony areas among patches of the *Eleocharis* and to a lesser extent *Damasonium*. Although the grass was rather uniformly distributed among *Eryngium*, it had dried too quickly here for proper seed set. The dried, leached grass stood in marked contrast to the grey-green plants in anthesis and fruit maturation which occurred in the deeper and barren areas of the lake basin.

5. Shasta County. *Orcuttia tenuis* occurs in abundance in a series of vernal pools around the Redding Municipal airport three to five miles north of Anderson, the area being known as Stillwater Plains. The southern series is largely in open grassland, while those to the west and north of the airport are surrounded by oak, digger-pine, and manzanita. The typical floristic association pattern of all of the pools can be illustrated by that in a single pool, a circular basin about 125 meters in diameter. Here *Eryngium* is marginal, but the majority of the bed contains *Eleocharis palustris* with intermittent patches of *Marsilea*. Although some of

the *Orcuttia* grew among the sedge, it was more common in the barren situations. None of the grass could be found among the *Eryngium*.

Two shallow and smaller pools associated with the open grassland had evidently dried too quickly, for the grass was leached and the spikelets were without seed. A small but deep ditch along the road and continuous with one of these basins contained green and properly maturing *Orcuttia*.

The type locality of *Orcuttia tenuis* is Goose Valley, north of Burney, Shasta County. The type collection was made here by Alice Eastwood in 1912, and since that time no other collections are known to have been made. This mountain valley is around 3500 feet in elevation, surrounded by mixed conifer forest, and is primarily meadowland with some dry-lake habitats in the northern section. Most of the valley is now largely cultivated, either as permanent pasture or cropland. A series of canals which effectively drain many areas is consequently disastrous to the survival of the *Orcuttia*. Fortunately, the grass was located in the nearly barren bed of an old ditch skirting a northeast portion of the valley (fig. 1-D). Aside from small patches of *Eleocharis palustris* and *Damasonium* along the edges, and some scattered *Downingia* and *Boisduvalia* in the bed, *Orcuttia tenuis* remained the dominant plant of the basin.

6. Lake County. The occurrence of *Orcuttia tenuis* in the Coast Ranges was first made known by Milo Baker, eminent Santa Rosa botanist, who collected the grass on the north shore of Bogg's Lake, Lake County. This lake is situated in a yellow pine forest flat on the northwest slope of Mount Hannah. The basin is around 1650 meters in diameter, contains water the year round, yet is provided with an adequate strand for the development of many unique and unusual plants.

A visit to the lake in August, 1958, proved disappointing because of the high water level and resultant flooded strand. Previous to 1958 the author had collected the grass on the southwest margin among *Eleocharis palustris* and *Eryngium* though it was exceedingly rare, requiring considerable search to locate perhaps two dozen plants.

III. YEARLY FLUCTUATIONS IN ABUNDANCE

The year 1958 was an ideal one for maximum development in the stands of *Orcuttia* and *Neostapfia*. In all of the areas visited, with one exception, these grasses were abundant, the most remarkable being the magnificent stand of *Neostapfia* just south of Modesto Lake.

What of other years? Even though the grasses must, in the overall floristic analysis, be regarded as rare and narrowly restricted endemics, why have they not been collected more often? The answer undoubtedly lies in their fluctuations in abundance from year to year. Unfavorable, dry years would be associated with poor development or scattered stands and earlier maturity. A shallow depth of water evaporating rapidly during the spring might prove quite disastrous to the annual stand of the grasses, even though they are situated in the required habitat. Such an environmental stress would antagonize the genetically-fixed, summer-

maturation character of *Orcuttia* and *Neostapfia*, resulting in heavy seedling mortality and consequent rarity of plants in the habitat. Furthermore, supposing good germination in water or on the mud of the vernal basins, too rapid a drying might cause premature flowering and poor to no seed set.

How, then, is perpetuation of the grasses maintained over unfavorable periods? Presumably the large seed production effected in such a year as 1958 might be adequate for the next several years, since there is a suggestion that the seed remain viable over many years and that a prolonged period of dormancy may be necessary before germination occurs. This supposition is drawn, but perhaps too hastily, from an attempt to germinate *Orcuttia* seed. *Orcuttia pilosa* grains collected in August, 1957, were placed on a blotter in a petri dish on January 31, 1958, kept at room temperature, and under continuous moisture. By September 1, 1958, no germination had occurred, though very few of them had succumbed to mold. Aside from the moisture, this artificial medium lacks all of the elements of the natural ones.

TABLE 1. Annual Precipitation (July to June) of four reporting stations in the Great Valley of California*

Season	Merced	Modesto	Sacramento	Red Bluff
1931-1952 (average)	12.35	12.44	16.68	23.15
1955-1956	15.42	15.62	25.53	28.53
1956-1957	7.40	8.63	13.78	12.25
1957-1958	25.63	23.04	28.70	38.03

* Data obtained from USDA Weather Bureau-Climatological Data, California section.

Table 1 shows some climatological data for most of the areas where the writer collected *Neostapfia* and *Orcuttia* in 1958. The amount of rainfall during the 1957-1958 season supports the argument that abundance of the two grass genera is dependent on the amount of precipitation. In all probability there was generally minimum development of the grasses during the 1956-1957 season. Dr. G. L. Stebbins, department of Genetics, and Dr. and Mrs. Louis Mann, department of Vegetable Crops, University of California, Davis campus, visited the vernal pool as shown in Figure 1-A, in the latter part of June 1957. They could scarcely find any *Neostapfia*, and what few plants were found were thoroughly dried and mostly dessicated. The remarkable solid stand of the grass present in July, 1958, could not have developed from the 1957 crop. Undoubtedly a larger seed crop had been produced in previous and more optimum years.

Without doubt, judging by observation of the excellent stands of both grass genera in 1958, the amount of rainfall and consequent depth of standing water in the vernal pools is most critical in their life cycle and reflects their yearly abundance.

The collections by Hoover (3) and others have pretty well established the geographical range of the *Orcuttia* species and *Neostapfia*. It remains

to round out their distribution by detailed collections of the two genera from year to year.

The primary purpose of this paper has been to stimulate interest in these most unusual and scientifically interesting grasses and make known their specific type of habitat and specific locations. The progress or decline of the grasses in any one area can be evaluated by the frequency of collection. This concern by the author is not without foundation. With the steady increase in California's population and with the resulting modified land manipulation that must occur, there is a good possibility of the destruction of many habitats, and this may result in the extinction of these grass species or their varieties.



FIG. 2. *Orcuttia mucronata* sp. nov. Plant from type specimen, approximately natural size.

IV. AN UNDESCRIBED SPECIES OF ORCUTTIA

The extensive collections of *Orcuttia* and *Neostapfia* made during July and August, 1958, uncovered a most unusual and distinctive *Orcuttia* species on the western side of the lower Sacramento Valley. The grass differs rather considerably from most other *Orcuttia* species, and a more radical treatment might erect a new genus. However, until all details of the plant can be evaluated it seems expedient to assign the grass to *Orcuttia*.

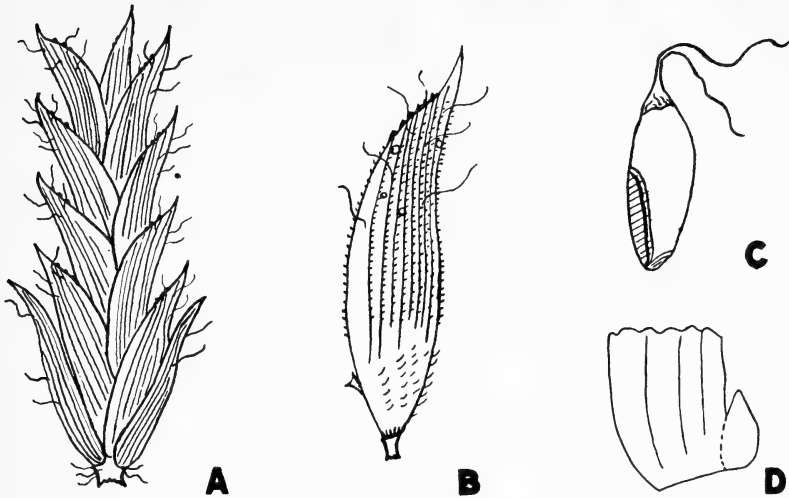


FIG. 3. *Orcuttia mucronata* sp. nov. (A) spikelet, $\times 5.5$. (B) floret, $\times 7.3$. (C) caryopsis, $\times 7.3$. (D) lodicule fused to the palea, $\times 18$.

***Orcuttia mucronata* sp. nov.**

Planta annua aestivalis aromatica flavoviridis folia rigida extrinsecus curvata 1–4 cm. longa inflorescentia racemiformis basi tantum inclusa spiculis 7–19 spiralibus 5–10 floribus nec supra nec infra glumas disarticulantibus lemmis 5–7 mm. longis apice mucro unico terminatis dentibus lateralibus suppressis palea apice trilobata lobis dentatis lodiculis duabus hyalinis enervatis paleae adnatis.

Summer annual; pilose throughout, yellow-green, aromatic. Culms few to many, decumbent, 2.5–12 cm. high; leaves eligulate, viscid, 1–4 cm. long, somewhat rigid, curved outward tapering to a fine point; inflorescence a raceme, 1.5–6 cm. long, partially included, spikelets 7–19 in number, spirally arranged; spikelets 7–13 mm. long, 5–10-flowered, no disarticulation between the florets or below spikelet; glumes 4–7 mm. long, unequal, nearly approximate, lanceolate, the apex pilose, mostly awn-pointed or occasionally with 1 or 2 lateral teeth; lemmas coriaceous, 5–7 mm. long, the upper portion excurved, sparsely pilose, scabrous, viscid and light green, the lower portion short-hairy and whitish, the apex obtuse with a median mucro, 0.5 to nearly 1 mm. long, the lateral teeth suppressed, the margin appearing merely erose; palea shorter than the lemma, the apex 3-lobed, the lobes toothed, pubescent towards the margin near the apex; lodicules 2, fused to the palea, hyaline, nerveless, about 0.25 mm. wide and 0.5 mm. long; anthers yellow fading pinkish; caryopsis oblong, flattened, 3 mm. long, the embryo 1.5–2.0 mm. long along one side of the grain (figs. 2 and 3).

Type. Alkaline lake, 12 miles due south of Dixon, Solano County, California, August 1, 1958, *Crampton 5057*, AHUC. (Isotypes: UC, JEPS, DS, US, CAS, K.) Known only from a single dry lake at the type locality.

Other collections (*Crampton 5011, 5059, 5093, and 5113*), all collected in this single locality, represent a series of developmental stages. *Orcuttia mucronata* is, at the most, rare. Only three patches of the grass, roughly 3–8 meters in diameter have been found over the large expanse of the lake bed. These small populations apparently occur in the deeper portions and on a cracked alkali with a brownish film over its surface. The white, smooth alkali pavement, characteristic of much of the lake harbored none of the grass. The soil type is classified as the Lindsey clay loam series. The soil survey of the Suisun area (1) indicates that the surface of this soil is a dull, dark or brownish grey material with a large proportion of fine to very fine sand. It deflocculates and when dry it becomes hard and baked. Organic matter is low, and most areas contain alkali. During the rainy season such areas become ponded for weeks or months at a time, the soil taking water slowly and having a high water-holding capacity. The surface layer extends from 8–10 inches in depth, and certain areas contain lime. The subsoil is heavy textured and compact, with some calcareous areas.

The soil at the area where the type plants of *Orcuttia mucronata* grow shows a pH of 8.0 on saturated paste as determined by the Agronomy Soils Laboratory.

V. MORPHOLOGICAL CHARACTERISTICS

The classical alliance of *Orcuttia* and *Neostapfia* to the tribe Festuceae, on the basis of gross spikelet morphology as outlined by Hitchcock and Chase (2), is inadequate in establishing relationship of the two genera to other grasses. A review of the salient features of both *Orcuttia* and *Neostapfia* indicates that they are not closely related to any members of the Festuceae.

One of the most conspicuous features of these grasses is the viscid secretion on all aerial parts of the plant whether young or mature. At first the secretion is glistening and watery, but towards maturity it becomes a thicker, denser, usually brownish exudate. In *Neostapfia*, distinctive scale-like raised glands on the lemma nerves and leaves contribute to the viscosity. In association with the copious secretion, a peculiar odor emanates from either fresh or dry material in any stage of development. The viscosity undoubtedly conserves plant moisture during the warm late spring and hot summer temperatures, while the aromatic habit may serve to reduce or repel animal depredation. In some of the collection areas grasshoppers were in abundance, but the green *Orcuttia* or *Neostapfia* plants were unaffected by the voracious insects.

In marked contrast to the Festuceae, *Orcuttia* and *Neostapfia* are summer-maturing annuals that occupy a highly specific type of habitat. Their coloration varies from a pale- to grey-green, and all are hairy. In

Neostapfia, however, hairs on the foliage are sparser, and very minute.

The nature of the foliage is distinctive, for in both genera there is no differentiation into sheath and blade, and consequently a true ligule and well-defined collar are absent. In all but *Neostapfia* and *Orcuttia mucronata* there is a definite abscission of the blade portion of the leaf. This deciduous character is not apparent until the leaves are dry, although in some instances the point of abscission is faintly visible in green tissue and might correspond to a "collar." The hairiness on the upper surface of the *Orcuttia* blades terminates abruptly at the fracture region, so that the resultant line of hairs might be construed as ligular. Otherwise the leaves of both genera loosely envelope the culms.

The culms of *Orcuttia* and *Neostapfia* are solid, the internodes being filled with pith. In the larger plants of *Neostapfia*, the decumbent culms form a zig-zag pattern, thereby providing additional support of the plant's superstructure. Branching is basal in all of the grasses except *Orcuttia tenuis*, which is literally "top-heavy." A single, filiform, culm, often with adventitious roots from the lower nodes, supports the entire ramification above, and when excessively branched the whole plant becomes decumbent.

The mature inflorescences in both genera are exserted, except for *Orcuttia mucronata*, which is partially included. *Neostapfia* has a cylindrical, spike-like panicle, the terminal portion differing from the rest of the rachis in bearing small, closely appressed, lanceolate bracts. In *Orcuttia* the inflorescences are spikes or racemes, the shape varying among the species. The spikes of *Orcuttia pilosa* and *Orcuttia tenuis* are more or less elongated, with mostly distichous spikelets. A spiral arrangement of spikelets exists in *Orcuttia greenei* and *Orcuttia mucronata*, with the inflorescence somewhat elongate. In *Orcuttia californica* var. *inaequalis* and *Orcuttia californica* var. *viscida* the spike is sub-capitate, with a second arrangement of spikelets.

The spikelets in *Neostapfia* are most unusual. They are without glumes, and the florets are so arranged as to suggest a trimerous cluster of spikelets. The florets are second, the two lower ones divergent, the three or four upper ones closely imbricate. Disarticulation normally occurs between the florets, but occasionally below the spikelets, the rachis being continuous. In *Orcuttia* the spikelets are solitary, the floret number variable from 5–10 in *Orcuttia mucronata* to 10–30-, or even 40 in other species. Except for *Orcuttia tenuis*, there is little or no disarticulation of the florets, the whole inflorescence largely non-shattering. The culms of *Orcuttia greenei* are excessively fragile at the base, and the mature seed heads are readily deposited upon the surface of, or cracks in, the adobe soil.

The form of the lemma apex is an excellent diagnostic character for both genera. Along with the form of the inflorescence, it is employed consistently in identification keys and will not be discussed here. The lemma texture in *Neostapfia* is papery except for the tough nerves, while the *Orcuttia* lemmas are coriaceous.

Mature grains of both genera were examined from the material collected during 1958. In common they show: a loose enclosure between the lemma and palea, lateral flattening with the embryo extending along one side, a large basal hilum, persistent style base at the apex, and compound starch grains in the endosperm. The *Neostapfia* grains are obovate, completely viscid, and dark brown in color. Those of *Orcuttia* are oblong, not or scarcely viscid, and the embryo and hilum are conspicuously brownish in contrast to the light-colored endosperm.

Lodicules are apparently absent in all except *Orcuttia mucronata*, and here their unique appearance (fig. 3-D) suggests that a sectional division should be made to accommodate this species in *Orcuttia*; or possibly the lodicules along with other characters suggest that generic rank is merited.

The similarity of habitats, growth habit, and convergence of some morphological features indicate a rather close relationship between *Orcuttia* and *Neostapfia*, while their affinity to other grasses is not readily apparent. They should be removed from the Festuceae and might well be considered as a separate tribe.

VI. SUMMARY

1. *Orcuttia* and *Neostapfia* are restricted to a special type of vernal pool or "hog-wallow" which limits their geographic distribution. The association patterns of both *Orcuttia* and *Neostapfia* are truly remarkable and would constitute excellent material for detailed ecological studies. In certain areas, as revealed by the preceding account, *Neostapfia* occurs with only certain species of *Orcuttia* or stands alone. Likewise, only rarely are two species of *Orcuttia* associated, but if so, one of them is represented by only a few scattered individuals. All, however, demand the relatively large vernal pool beds for successful perpetuation.

2. It is suggested that their varying abundance from year to year is dependent upon the amount of rainfall and upon a long period of seed viability.

3. Morphological developments are a natural consequence of the environment with specializations directed towards viscosity, aroma, pubescence, and non-shattering inflorescences. Both genera are closely related, undoubtedly forming a natural grouping among the grasses, though their relationship to others is rather obscure.

4. A new species of *Orcuttia* from Solano County is described and illustrated.

Agronomy Herbarium
Department of Agronomy
University of California, Davis

BIBLIOGRAPHY

1. CARPENTER, E. J. and S. W. CROSBY. 1930. Soil Survey of the Suisun area. U. S. Dept. Agric. Bur. Chem. & Soils. Series 1930, Number 18: p. 33.
2. HITCHCOCK, A. S. and AGNES CHASE. 1950. Manual of the grasses of the United States. 2nd Edition. USDA Misc. Publ. 100.
3. HOOVER, ROBERT F. 1941. The genus *Orcuttia*. Bull. Torrey Club 68 (3):149-156.

THE TAXONOMIC RELATIONSHIP BETWEEN PICEA GLAUCA (MOENCH) VOSS AND *P. ENGELMANNII* PARRY¹

T. M. C. TAYLOR

For many years botanists and foresters have been puzzled and frustrated by the spruce complex in British Columbia, particularly the plexus centering around *Picea glauca* (Moench) Voss (White spruce) and *P. engelmannii* Parry (Engelmann's spruce). In the northern parts of the province *P. glauca* appears in its typical form and is a clear-cut entity. At higher altitudes in the southern interior of the province *P. engelmannii* may be found in equally characteristic form. Unfortunately, between these two easily distinguishable extremes there is a great range of intermediates. The taxonomic, and hence the nomenclatural, disposition of these intermediates is the substance of the present paper.

Materials studied were collected largely at Banff, in the Upper Columbia Valley, and in the Cranbrook-Moyie Lake area. This southeastern region of the province and adjacent Alberta was selected because here the problem raised by the intermediate forms of spruce is particularly acute. Collections were made with the primary purpose of gaining a statistical picture of the variability between individual trees of certain mensural characters of leaves and cones. It was felt that only when the extent of variation within the individual was established, could one proceed with confidence to generalizing from small samples drawn from many trees.

Materials were collected from about seventy randomly selected trees. In case the degree of shading might produce constant differences, cones and twigs with needles were taken from both the north and south side of trees. Needles were also collected from both vegetative and reproductive shoots. Statistical analysis showed no significant difference between samples from the north and south side, nor between needles from reproductive and vegetative twigs. In the present report therefore this distinction is not maintained.

The difficulty of making accurate measurements of curved leaves was overcome by boiling them for five minutes to render them pliable so that they could be straightened out. Spreading of the scales in dry cones also offered complications for measurement but these complications were also overcome by boiling the cones until they sank. By this time the scales had contracted and were closely appressed in the cone. It was established that prolonged boiling produced no further change in dimensions.

Mention may be made of the findings on intra-tree variability. Needle lengths, with means of the order of 13.5 mm. and standard deviations of about 2 mm. showed coefficients of variability ranging from about 11 to 20. Cone diameters with means of the order of 13.5 mm. have standard deviations of slightly over 1 mm. with a range in the coefficients of vari-

¹ This study was supported in considerable measure by financial assistance from the National Research Council of Canada to which body grateful acknowledgment is made.

ability from 6 to 10. Cone lengths were about 42 mm., with standard deviations about 3.5 mm. and variability with coefficients about the same as for diameters.

One can conclude then that needle lengths are very variable on the same tree and that a large number would have to be measured in order to obtain a statistically satisfactory mean value. Cones, on the other hand, are much more uniform in dimensions and so smaller samples per tree would be acceptable.

The most obvious difference between Engelmann's and White spruce is in the cone scale. Those of the former are thin and somewhat papery, wedge-shaped with wavy to erose margins, and commonly erose to truncate at the apex. The scales of the White spruce on the other hand, are obovate-triangular, somewhat stiff with entire margins, the apex being rounded or somewhat flattened, not erose. It was possible to interpolate three classes of intermediates between these extremes. In the accompanying tables the five cone type classes are numbered in Roman numerals with *P. engelmannii* I and *P. glauca* V. Table 1 shows the means and standard deviations of cone diameters and lengths for the five cone type classes. The differences between the means of diameter are not reliable while the differences in mean length of types I and V is reliable at the level of .01. The erratic means of length for types II, III and IV are presumably due to inadequacy of the samples. This, however, is a matter that requires further investigation.

TABLE 1. Relationship between cone dimensions and cone type in *Picea engelmannii*, *P. glauca*, and intermediates.*

Cone type	Diameter				Length			
	M	SD	N	n	M	SD	N	n
I	13.7	1.13	14	521	45.0	3.11	14	518
II	14.0	1.12	12	349	46.1	6.57	11	328
III	13.4	1.03	6	207	41.8	3.72	6	199
IV	13.6	1.28	6	368	43.1	3.00	6	377
V	13.4	1.27	21	1449	41.4	3.96	21	1491

* I represents *P. engelmannii*, V, "*P. glauca*," II-IV, intermediates. M = mean (in mm.), SD = standard deviation (in mm.), N = number of trees sampled, n = number of cones measured.

Analysis of needle length showed no significant differences between the means for the different cone types. Engelmann spruce needles, however, tended to be straight and slender, acuminate and somewhat square in cross-section, while those of White spruce were firmer, often curved and rounded at the apex, tending to be dorsiventrally flattened or triangular in section. Needles with these characteristics in other combinations were classed as "intermediates." Table 2 shows the relationship found between leaf type and cone type. It is apparent that foliage characters are not correlated with cone types and are probably due to the independent segregation of several genes.

TABLE 2. Relationship between leaf type and cone type in *Picea engelmannii*, *P. glauca*, and intermediates.*

Leaf types	Cone types					N
	I	II	III	IV	V	
'engelmannii'	9	7	5	----	----	21
intermediate	12	4	4	7	8	35
'glauca'	----	----	----	1	13	14
Totals	21	11	9	8	21	70

* I represents *P. engelmannii*, V, *P. glauca*, II-IV, intermediates. N = number of trees sampled.

The relationship between the indumentum of the twigs and cone types was also studied. Twigs of White spruce are characteristically glabrous, while those of Engelmann's spruce have a short, crisp pubescence. In Table 3 it can be seen that all cone types may be borne on trees with pubescent twigs, except that cone type V has an equal chance of being borne on a tree with glabrous twigs. One can speculate that the development of indumentum is controlled by a single pair of genes and that "pubescence" is dominant.

TABLE 3. Relationship between indumentum of twigs and cone in *Picea engelmannii*, *P. glauca*, and intermediates.*

Twigs	Cone types					N
	I	II	III	IV	V	
Pubescent	21	10	9	8	11	59
Glabrous	----	1	----	----	10	11
Totals	21	11	9	8	21	70

* I represents *P. engelmannii*-type, V, *P. glauca*-type, II-IV, intermediates. N = number of trees sampled.

It is apparent that White and Engelmann's spruce are very much alike and that even such diagnostic features as mean cone length, and shape and character of the scales are merely the extremes of a series of intermediates. Both 'engelmannii' and 'glauca' needle types are found on trees with 'intermediate' type cones and 'intermediate' type needles may be associated with any type of cone. Glabrous twigs have only been found on trees with 'glauca' cones but, on the other hand, there is an equal chance that the twigs on such trees will be pubescent. On several occasions in the past it has been commercially important to try to distinguish lumber cut from these two spruces. No differentiating histological details have been found and Barton and Gardner (1957), using partition chromatography in addition to infra-red and ultra-violet spectrographic methods, failed to establish any chemical differences between the woods.

Wright (1955) has examined in considerable detail the question of interspecific hybrids in *Picea*. In his paper he attempts "to correlate species

crossability with geographic distribution, morphology, and phylogeny." He examined thirty-one species with respect to fifty-one characters that show differences between some or other of these species. The majority of the characters, of course, do not lend themselves to measurement and are to quite an extent subjective. It is regrettable that Wright's observations were not analyzed statistically. Had they been, the relationship between *P. glauca* and *P. engelmannii* would likely have appeared very much closer than he concludes.

Wright (1. c.) has made some investigation of hybridizing between White and Engelmann spruce. Using a hybridity index, he shows that very considerable introgression is taking place over a wide area extending from latitude 51° to 58° N. and between longitude 109° to 124° W. That these intermediates are almost certainly of hybrid origin is borne out by his report of successful reciprocal crosses between the two species.

Garman (1957) has made a detailed morphological and distributional study of spruce populations in British Columbia. Using a "morphological index" on which pure *P. glauca* rates 6 and pure *P. engelmannii* rates 18, he shows the very extensive geographic area occupied by intermediates on this scale. This index has apparently proven useful in distinguishing populations, but its value would be greatly enhanced if the mensurable characters had been treated statistically. Only average values and ranges of measurement are given and, as the latter frequently overlap, their significance cannot be evaluated.

In the opinion of the present author, the phylogenetic relationship between *P. glauca* and *P. engelmannii* is best indicated by regarding them as subspecies of a single species and so the following changes in status are proposed. According to the provisions of Article 57 of the International Code of Botanical Nomenclature (Lanjouw 1956) *Picea glauca* (Moench) Voss, which has priority, becomes the legitimate name when the two species are combined into one.

PICEA GLAUCA (Moench) Voss subsp. *glauca*

Abies canadensis Mill. Gard. Dict. Ed. 8, Abies No. 4, 1768; *nomen confusum*

Pinus glauca Moench, Verzeichn. Bäume Weissenst. 73. 1785

Pinus alba Ait. Hort. Kew. 3:371. 1789

Picea laxa Sargent, Gard. and For. 2:496. 1889

Picea glauca (Moench) Voss, Mitt. Deutsch. Dendr. Ges. 1907:93. 1907

Picea glauca var. *porsildii* Raup, Sargentia 6:102. 1947

PICEA GLAUCA (Moench) Voss subsp. *engelmannii* (Parry) stat. nov.

Abies engelmanni Parry, Trans. Acad. St. Louis 2:122. 1863; *nomen nudum*

Picea engelmanni Parry ex Engelmann; Trans. Acad. St. Louis 2:212. 1863

Picea columbiana Lemmon, Gard. and For. 10:183. 1897

There is little doubt that *Picea glauca* var. *albertiana* (S. Brown) Sargent (*Picea albertiana* S. Brown, Torreya 7:126. 1907) is based on an individual of the hybrid swarm between subsp. *glauca* and subsp. *engelmannii* and in consequence this name should no longer be perpetuated. When reference is made to these hybrid intermediates it should be done

by employing a formula as provided by Article H.2 of the International Code with particular attention to the "Note."

Goodman (1950), in describing his *P. engelmannii* var. *glabra*, almost certainly had at hand a biotype of Engelmann's spruce that showed the result of the introgression of genes from the glabrous White spruce.

Department of Biology and Botany,
University of British Columbia,
Vancouver, Canada

LITERATURE CITED

- BARTON, G. M. and J. A. F. GARDNER. 1957. Comparison of the heartwood extractives of *Picea glauca* and *Picea engelmannii*. *Forestry Chron.* 33(2):136-138.
- EKLUNDH, G. 1943. Artkorsningar inom sl. *Picea* . . . tillhörande fam. Pinaceae. *Svensk Papp Tidn.* 46:55-61, 101-105, 130-133. (Species crosses within the genera *Picea*, etc.) (Sw.) In *Forestry Abstr.*, V. abs. 95.
- GARMAN, E. H. 1957. The occurrence of spruce in the interior of British Columbia. *Brit. Col. Forestry Service Tech. Publ. T.* 49:1-31.
- GOODMAN, G. J. 1950. A New Variety of Engelmann Spruce. *Madroño* 10:177.
- JOHNSON, L. P. V. 1939. A descriptive list of natural and artificial hybrids in North American forest-tree genera. *Canad. Jour. Res. C.* 17:411-444.
- LANJOUW, J., editor. International Code of Botanical Nomenclature adopted by the Eighth International Botanical Congress, Paris, July, 1954. Utrecht.
- WRIGHT, J. W. 1955. Species crossability in spruce in relation to distribution and taxonomy. *Forest Sci.* 1:319-349.

FIELD STUDIES OF NATURAL HYBRIDIZATION IN THE OREGON SPECIES OF IRIS L. SUBSECTION CALIFORNICAE DIELS

QUENTIN D. CLARKSON

Smith and Clarkson (1956) have discussed the cytological aspects of hybridization in *Iris*, subsection *Californicae*. They reported that, with the exception of *I. tenuis* Wats., which has been removed to a new subsection (Clarkson, 1958), all the members of the subsection studied had a uniform chromosome morphology, and all contained a diploid number of forty. Fertile hybrids were produced experimentally without difficulty and all were highly fertile except that hybrids involving *I. tenuis* as a parent could not be produced. This paper will discuss some natural hybrids of those taxa occurring in western Oregon and will propose certain nomenclatural revisions. Because the subsection was treated taxonomically by Foster (1937), conventional citations will not be included except for taxa described since that time.

DISTINGUISHING CHARACTERISTICS. Aside from the usual characteristics of the genus *Iris*, the members of the subsection *Californicae* are distinguished by a usually deltoid stigma; D-shaped, cubical or ovoid seeds; the absence of foliaceous stem leaves; and tough basal leaves which are reddish at base. A number of characteristics have been used for distin-

guishing species by various authors, including Foster (1937) and Dykes (1912) in the two most complete reviews of the subsection. These have been evaluated with herbarium specimens (Clarkson, 1950) and with living material. Those characters which allow ready distinction of taxa and which are most easily utilized for study of hybrids are as follows:

Perianth. The petals are usually narrow and about the same length as the sepals which are linear to spatulate in shape. Color of the perianth ranges from white, purple, pale yellow, golden yellow, to apricot and maroon.

Perianth tube and pedicel. The perianth tube varies in length from 0.4 to 12 centimeters with the pedicel varying approximately inversely.

Bracts of the inflorescence. The bracts, or spathes, are variable in shape from ovoid to linear; in length from 2 to 15 centimeters; and in position from opposite to alternate.

FIELD STUDIES. Although a quantitative study of morphological and ecological characteristics was desirable, inadequate knowledge of distribution of the species and the absence of definite knowledge of natural hybrids made such work impossible. Field work was therefore conducted on a qualitative basis. A limited number of transplants made during current field work and previously by Smith (Smith and Clarkson, 1956) demonstrate that the characteristics of the taxa are constant under varying environmental conditions. Herbarium specimens designed to represent all the variation present in a given location were collected. These mass collections are in the possession of the author.

Results of field studies are given below together with interpretations of their significance.

HYBRIDS BETWEEN *I. TENAX* AND *I. CHRYSOPHYLLA*

Iris tenax is characterized by narrow, distant bracts; a perianth tube from 4 to 9 millimeters in length and by lavender to purple flowers with broad spatulate sepals. The plants are tall and with definite stems. Though the species is typically purple-flowered, two yellow-flowered populations have been found. One of these is along Scoggin's Creek in Washington County, Oregon. It has been treated as *I. gormanii* Piper and more recently as *I. tenax* var. *gormanii* (Piper) Foster. The second yellow-flowered population is on Monument Peak, Linn County, Oregon. This local population is apparently not well known and has not been cited in the literature of the subsection. Neither of these populations can be distinguished from the typical phase of *I. tenax* by any trait other than color.

The general range of the species is from the central part of western Washington to southern Oregon. Ecologically it is a species of unshaded conditions and is abundant on the oak-covered hills of the Willamette and Umpqua valleys. It does not extend into coniferous areas unless trees are cut, roads built, or conditions otherwise disturbed in such a way that shading is reduced. Within the general range there seem to be no soil or moisture factors limiting its distribution. Factors controlling the northern and southern limits of the species range are probably climatic in nature.

Iris chrysophylla is characterized by lanceolate, opposite bracts; a perianth tube 5 to 9 (occasionally to 12) centimeters in length; a pedicel less than 1 centimeter in length; and by pale yellow flowers with narrow perianth parts. In southwestern Oregon, where the species is most abundant, well-marked stems are produced. In the Cascade Mountains of northern Oregon, the plants are often nearly stemless. Plants at two previously unreported stations of the species, Mill Creek, Polk County, Oregon, and Prairie Mountain, Benton County, Oregon, are of the Cascade type.

Ecologically *I. chrysophylla* is a species of open coniferous forests. It grows best on drier soils and will tolerate more shade than *I. tenax*. It is a characteristic species of the ponderosa pine and ponderosa pine-Douglas fir communities of southwestern Oregon.

Distinctive hybrids between *I. tenax* and *I. chrysophylla* have been found in three locations: (1) $4\frac{1}{2}$ miles up Mill Creek from the Dallas—Wallace Bridge highway, Polk County, Oregon; (2) $13\frac{1}{4}$ miles southwest of Roseburg, Douglas County, Oregon, along Oregon State highway number 42; (3) steep hills along the first tributary of the North Santiam River west of the Detroit Dam, Marion County, Oregon. In all three locations conditions have been disturbed by road construction.

At all three of these sites individuals have been found which are intermediate between the parent species and which cannot be assigned to either species. Bracts of the hybrids are opposite and are broader than is characteristic of *I. tenax* but not so broad as those of *I. chrysophylla*; flower color is maroon to grayish-lavender; and the perianth parts are slender. The plants are smaller than typical *I. tenax* but have a definite stem. Perianth tube length in the natural hybrids averages 2.2 centimeters and the pedicel averages 1.4 centimeters. Comparative measurements in the known hybrids are perianth tube 2.5 and pedicel 1.8. This indicates that the hybrids are possibly of the F_1 generation. In other characters the natural hybrids compare closely with the known hybrids.

The area of overlapping ranges is, in all three cases, small. At Mill Creek and along the North Santiam highway, a transect of less than 100 yards extends through the area occupied by both species. At the site southwest of Roseburg, a similar transect extends less than one-half mile.

Hybrids between these two species appear to be introgressive toward *I. tenax*. Individuals identifiable as *I. tenax* show definite *I. chrysophylla* characteristics for at least ten miles from the area where typical *I. chrysophylla* occurs. These individuals exhibit a change in color toward a pale purple; a reduction in size; and a tendency toward broader and less distant bracts. These modifications in *I. tenax* are what might be expected as a result of hybridization with *I. chrysophylla*. The intermediates previously discussed are found in the areas where the two species occur together but *I. chrysophylla* remains constant and no individuals of that species have been found which exhibit *I. tenax* characteristics.

Introgressive hybridization between these two species is a close parallel

of a situation described by Anderson (1949) in which hybridization is followed by backcrossing and selection of backcross types. Apparently, in this case, only the offspring of the intermediate \times *I. tenax* backcross are selected. The factors of the ecology which bring about this selection are not known. The introgression, however, has resulted in a considerable increase in the variability of *I. tenax* while *I. chrysophylla* has remained constant.

The occurrence of *I. chrysophylla* at two locations in the Coast Range of Oregon was not unexpected. The presence of individuals of *I. tenax* with lanceolate, opposite bracts in the Coast Range west of Corvallis, Oregon, suggested possible hybridization with *I. chrysophylla*. At the Mill Creek location in Polk County, Oregon, the two species are in contact at the present time, as was previously mentioned. At Prairie Mountain, Benton County, Oregon, there is no present day contact on the north and probably not on the south. *Iris chrysophylla* is abundant on a broad, well-drained meadow, along a south-facing slope near the summit of Prairie Mountain at an elevation of about 3200 feet. *Iris tenax* is not now in contact on the north, presumably because of the dense growth of Douglas fir on that side. The south side of the mountain is more open and the two species may come together though no intermediates have been found. *Iris tenax* specimens collected at Horton, Lane County, eight miles to the south, have a narrower and more pale perianth which suggests hybridization with *I. chrysophylla*.

Thirty miles north of Prairie Mountain are individuals of *I. tenax* with linear-lanceolate, opposite bracts, and narrow, pale purple perianth parts. These plants are probably the result of introgression from *I. chrysophylla* to *I. tenax*. These hybrid forms indicate either that *I. chrysophylla* is more abundant in the Coast Range than is now known or that it was more abundant in the past and has survived only on the more favorable sites. Either hypothesis may be true in part, but it seems unlikely that these forms are the result of recent hybridization. *Iris chrysophylla* has not been found in the Coast Range between Prairie Mountain and Mill Creek, and distances are probably too great for plants at those locations to be involved as parents. The most probable explanation is that *I. chrysophylla* was more abundant in the Coast Range of northern Oregon in the past and has remained only at the dry, open sites such as Mill Creek and Prairie Mountain. The occurrence of a warm, dry period in postglacial times, followed by general cooling and increase in moisture (Hansen, 1947) makes this a reasonable assumption. Whether *I. chrysophylla* was distributed throughout the general area of northwestern Oregon in the past or only on the higher peaks, is a question which cannot be answered. In either case, abundant opportunities for hybridization could have existed. Introgression, such as occurs today, could have given greater adaptive value to *I. tenax* while *I. chrysophylla* remained more nearly constant and more vulnerable to environment change.

There is, however, no reason to suppose that the yellow-flowered forms

of *I. tenax* on Monument Peak and in Washington County, Oregon, are of hybrid origin. All the hybrids between these two species, including the artificial hybrids produced for this study, exhibit a tendency toward the lanceolate, opposite bracts of *I. chrysophylla*. The purple flower color is reduced to greyish-lavender in the known F_1 hybrids, and none of the hybrids found in nature have yellow flowers. An independent origin for this color trait is not improbable as evidenced by *I. hartwegii*, which is closely related to *I. tenax* and has yellow flowers and by the fact that there are yellow-flowered forms in *I. macrosiphon* which is otherwise purple-flowered.

HYBRIDS BETWEEN *I. DOUGLASIANA* AND *I. INNOMINATA*

Iris douglasiana is a tall species averaging about 60 centimeters in height and is characterized by leaves about a centimeter wide; a branching stem; lanceolate, opposite bracts; large pale purple to white flowers; and a perianth tube 1 to 2 centimeters in length. Two or three flowers per branch are produced. Distribution of the species in Oregon is limited chiefly to a narrow, open coastal strip from Coquille, Coos County, southward. The species normally extends inland only along river valleys. It has not been seen in dense shade.

Iris innominata is a low species averaging about 35 centimeters in height and is characterized by narrow leaves which are about 4 centimeters wide; simple stems; ovate, opposite bracts; small, golden yellow flowers; and a perianth tube 1 to 2.5 centimeters in length. Distribution of the species is limited to the open meadows and hills of southern Douglas, Coos, and Curry counties, Oregon.

Hybrid colonies of about 100 plants each of the *I. douglasiana* \times *I. innominata* cross have been found along Saunder's Creek, Curry County, Oregon. The two sites are $1\frac{1}{2}$ and $2\frac{1}{2}$ miles from the Rogue River, 3 miles upriver from Gold Beach on the south side of the Rogue River. The colonies are found in cut-over forest land with most of the plants completely exposed to the sun, though a few are found in the shade of *Umbellularia californica*. Some of the individuals are similar to the known hybrids grown for cytological study. Perianth size and plant size appear to be intermediate between the parent species and the bracts are shorter and more ovoid than are those of *I. douglasiana* but are longer and narrower than those of *I. innominata*. These individuals may be F_1 hybrids. Other plants appear to be the result of backcrossing and segregation.

Aside from the demonstration of genetic continuity between species, the taxonomic significance of the hybrids is considerable. Some individuals from one of the hybrid colonies compare closely with individuals referred to *I. thompsonii* Foster. There is a strong suggestion of the hybrid origin of that taxon. *Iris thompsonii* has been collected along the Rogue River and along United States Highway 101 from Carpenterville to Brookings, Curry County, Oregon. In California, it has been collected along the Smith River, northeast of Crescent City, Del Norte County. The

species can be distinguished from *I. innominata* by the more lanceolate bracts and by the pale purple to lavender flower color. It also seems to be taller, averaging about 45 centimeters. These are characteristics which could be fixed by backcrossing of the *I. douglasiana* \times *I. innominata* hybrids to *I. innominata*.

A similar hypothesis can be erected to explain those specimens with more ovate bracts and lavender-grey flowers referred by Foster (1937) to a new variety, *I. douglasiana* var. *oregonensis*. Backcrossing of the intermediates of the *I. douglasiana* \times *I. innominata* cross to *I. douglasiana* could result in the fixing of these *I. innominata* traits in otherwise typical *I. douglasiana*.

While both assumptions are largely hypothetical, they are lent support by the occurrence of these variants in an area where the two species come together and hybridize. The only barriers seem to be ecological, though exact factors cannot be stated. The removal of the forest trees with the accompanying reduction in shade has apparently removed the barrier to hybridization in the case discussed here, but elevation and soil factors may be important in other locations. However, hybrids probably will be found wherever the hills of Coos and Curry counties are near the ocean and conditions are disturbed or where *I. douglasiana* extends inland along river valleys. In these areas, at least, the two species can be expected to occur together.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. THOMPSONII*

Iris bracteata is a tall species averaging about 50 centimeters in height and with a thick perianth tube 0.5 to 1.0 centimeter in length, a pedicel 3 to 6 centimeters long, and golden yellow flowers. Typically the leaves are a glossy green on the upper surface and glaucous on the lower. The species has been seen only in southwestern Josephine County, Oregon, and northeastern Del Norte County, California. Ecologically it is restricted to shaded places. The species is found in greatest abundance within ponderosa pine communities, but it is sometimes found on cut-over forest land under a cover of bracken fern.

Iris thompsonii has been discussed as a possible hybrid segregate of the *I. douglasiana* \times *I. innominata* cross. Colonies are best developed along the lower Smith River, from 12 to 15 miles northeast of Crescent City, California. In this location, the colonies are well established on open rocky hillsides, and have not been seen in the shade.

Proceeding northeastward from Jedediah Smith State Park in Del Norte County, over the Siskiyou Mountains into Oregon, the colonies become more shade tolerant. Color changes gradually from predominantly pale purple flowers to predominantly yellow flowers, though a few white-flowered plants are present. Bract characteristics appear to be intermediate between the two species, changing gradually from ovoid and 5 centimeters long, to narrower and 7 centimeters long. Height of the plant also becomes progressively greater as colonies nearer typical *I. bracteata* are

examined. Three miles north of the summit of the Siskiyou Mountains only typical *I. bracteata* has been seen.

No individuals similar to the known F_1 hybrids have been found in nature. The transition between the two species is gradual, probably because of ecological requirements which permit more hybridization and survival of most of the hybrid offspring.

HYBRIDS BETWEEN *I. BRACTEATA* AND *I. CHRYSOPHYLLA*

Distinct hybrids between these two species have not yet been clearly demonstrated. Despite the pronounced morphological differences between the two, only one individual has been secured which can be considered intermediate. The relationship of the perianth tube to the pedicel is reversed in these two species. *Iris chrysophylla* has a perianth tube 5 to 6 times longer than the pedicel. In *I. bracteata* the pedicel is 5 to 6 times longer than the perianth tube. In the intermediate specimen cited above, the pedicel is twice the length of the perianth tube, clearly not characteristic of either *I. chrysophylla* or *I. bracteata*. This specimen was collected near Bridgeview, Josephine County, Oregon, where the two species occupy the same general area.

Complementing this admittedly limited evidence, field examination reveals hybrid characteristics which are not readily demonstrable with pressed specimens. Near Cave Junction, Josephine County, there are individuals of *I. bracteata* with narrow perianth segments characteristic of *I. chrysophylla*. The hybrid origin of these individuals is supported by the fact that all the known hybrids involving *I. chrysophylla* as a parent exhibit the narrow perianth of that species. There are also individuals, in the Cave Junction area, of *I. chrysophylla* with perianth color similar to the golden yellow of *I. bracteata*. The known *I. bracteata* \times *I. chrysophylla* hybrid has golden-yellow flowers and all other crosses involving golden-yellow and pale yellow-flowered parents show the flower color of the golden-yellow parent.

TAXONOMY. Due to the absence of cytological barriers between taxa and the presence of natural hybrids, nomenclatural revision which will better reflect the biology of the organisms seems necessary. Therefore, the following new combinations are proposed. Further field work is needed before accurate limits can be set for the California members of the subsection and they will not be considered here.

1. **IRIS TENAX** Dougl. subsp. **TENAX** (*I. tenax* Douglas ex Lindley, Bot. Reg. xv. t. 1218, 1829). This subspecies includes the typical form which has been discussed previously in this paper as *I. tenax*. Also included, without nomenclatural distinction, is the yellow-flowered *I. tenax* var. *gormanii*. The yellow-flowered form from Monument Peak, Linn County, Oregon, will be included within *I. tenax gormanii* and therefore within *I. tenax tenax* without nomenclatural distinction.

2. **IRIS TENAX** subsp. **CHRYSOPHYLLA** (Howell) (*I. chrysophylla* Howell, Fl. N.W. America 1:633, 1902). No type specimen was designated

for Howell's *I. chrysophylla*. However, filed with the type specimen collection at the herbarium of the University of Oregon is a specimen labeled "Type specimen" in the distinctive handwriting of Thomas Howell. This specimen, collected at Grants Pass, Josephine County, Oregon, in May 1887, must be considered the type specimen for Howell's species and therefore for the proposed subspecies.

3. *IRIS TENAX* subsp. *BRACTEATA* (Watson) (*I. bracteata* Watson, Proc. Amer. Acad. 20:375, 1885). This subspecies includes the species as described by Watson.

4. *IRIS TENAX* subsp. *DOUGLASIANA* (Herbert) (*I. douglasiana* Herbert, Bot. Beechey Voy. 395, 1841). Included in *I. tenax douglasiana* without nomenclatural distinction is *I. douglasiana* var. *oregonensis* Foster. So long as it is understood that Foster's variety is probably of hybrid origin, there is no need to distinguish a form which obviously belongs to what has been described as *I. douglasiana*. Since this subspecies is found in California as well as Oregon, this new combination must necessarily include the California plants. This does not mean that the California plants of this taxon should be ignored in any further study. There is undoubtedly considerable variation present that is not included in the Oregon representatives.

5. *IRIS TENAX* subsp. *INNOMINATA* (Henderson) (*I. innominata* Henderson, Rhodora 32:23, 1930). This subspecies has been retained as originally described except for the reduction in rank.

6. *IRIS TENAX* subsp. *THOMPSONII* (Foster) (*I. thompsonii* Foster, Rhodora 38:199, 1936). The only real difference between this proposed new subspecies and *I. tenax innominata* is in the purple flower color of *I. tenax thompsonii*. Since it has been suggested that *I. tenax thompsonii* may be of hybrid origin with *I. tenax innominata* as one parent, a close morphological relationship is to be expected. The two taxa differ slightly in distribution, *I. tenax thompsonii* is a species of elevations between 400 and 1000 feet while *I. tenax innominata* is usually at sites over 1500 feet. For that reason and because *I. tenax thompsonii* does form distinct colonies, it is retained.

Division of Science,
Portland State College,
Portland, Oregon

LITERATURE CITED

- ANDERSON, E. 1949. Introgressive hybridization. Wiley and Sons. New York.
CLARKSON, Q. D. 1950. Population studies in *Iris*. M.S. thesis. University of Oregon. Eugene.
———. 1958. *Iris* section *Apogon* subsection *Oregonae*. Subsect. Nov. Madroño 14:246-247.
DYKES, W. R. 1913. The genus *Iris*. Cambridge University Press. London.
FOSTER, R. C. 1937. A cyto-taxonomic survey of the North American species of *Iris*. Contr. Gray Herb. 119:1-82.
HANSEN, H. P. 1947. Postglacial forest succession, climate and chronology in the Pacific northwest. Trans. Am. Philos. Soc., N.S. 37, part 1:1-130.
SMITH, F. H. and Q. D. CLARKSON. 1956. Cytological studies of interspecific hybridization in *Iris*, subsection *Californicae*. Am. Jour. Bot. 43:582-588.

VARIATION PATTERNS IN FOUR CLONES OF
MERTENSIA CILIATA¹

JEANETTE S. PELTON

Mertensia ciliata (James) G. Don is well delineated from other species of the genus in the monograph by Williams (1937). Field observations in the area of the present study, Gunnison County, Colorado, bear out this distinctness of *M. ciliata* from other sympatric species, although considerable intraspecific variation is easily detected. In spite of the fact that certain other species of the group grow sympatrically in the study area with *M. ciliata*, five years of observation by the author have not uncovered a single likely instance of hybridization between *M. ciliata* and any of the other species. Nor did artificial cross pollination produce any fertile seed between *M. ciliata* and *M. fusiformis* Greene. In the observed populations, therefore, *M. ciliata* seems an excellent species in which to study quantitatively intraspecific variation patterns which are probably uncomplicated by any present inflow of genes from another species. With this objective in mind, three floral characteristics within and among four clones of *M. ciliata* were chosen for study. The clones were selected such that each was separated from the other by a distance of one-third to two miles. Such a distance probably assures that each clump is an individual clone with a different genetic origin. Hence the four clumps will be referred to hereafter as clones A, B, C, and D. Since each clone was growing in a different combination of environmental factors, at least four of the many micro-habitats to which individuals of *M. ciliata* are adapted are represented. By selecting clones in the above manner, it was presumed that a measure of somatic variability could be obtained, since the phenotypic measurements would be made upon single genotypes each produced in a slightly different environment. In addition, differences in gene expression among the clones imply possible genetic variation patterns.

METHODS AND RESULTS

Clones A, B, C, and D were collected in the summer of 1953 in or near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. No clone was nearer than approximately one-third mile from another, and all clones were located on different drainage channels. The altitude is approximately 9,500 feet for three of the clones and 10,000 feet for Clone B. Voucher specimens of the collections are in the personal herbarium of the author.

Length of calyx, corolla-tube, and corolla-limb were measured from these herbarium voucher specimens. In this study the corolla-limb, as defined by Williams (1937), will include that portion of the corolla above the fornicis. Individual mature flowers were measured for the three floral characteristics to 0.5 mm. using low power of a binocular microscope to

¹ The author is grateful for the use of facilities of the Rocky Mountain Biological Laboratory and to Dr. John F. Pelton for criticisms and additions to the manuscript.

TABLE 1. Arithmetic mean, standard deviation, and range of variation for length of calyx, corolla-tube, and corolla-limb in four clones of *Mertensia ciliata*

Clone	No. of Individuals	Calyx Length			Corolla Tube Length			Corolla Limb Length		
		Mean	Standard Deviation	Range of Variation	Mean	Standard Deviation	Range of Variation	Mean	Standard Deviation	Range of Variation
A	150	2.5	0.24	2.0-3.5	5.4	0.52	3.5-6.5	5.9	0.70	4.5-8.0
B	94	1.8	0.30	1.5-2.5	6.2	1.51	5.0-7.5	7.3	1.04	5.0-9.5
C	132	1.8	0.33	1.5-2.5	6.8	0.50	5.5-8.0	6.1	0.88	4.0-8.0
D	40	2.1	0.30	1.5-2.5	5.9	0.36	5.0-6.5	7.1	0.79	5.0-9.0

increase accuracy. Arithmetic mean, standard deviation, and range of variation were determined for each characteristic measured in the four clones. These results are presented in Table 1. In Figure 1 variation among the four clones is diagrammed using mean length of calyx, corolla-tube and corolla-limb. Range of variation within the clones is diagrammed in Figure 2.

Descriptions of the clones are as follows:

CLONE A. Collected July 15 from a moist roadside site one-fourth mile north of the laboratory. The clump was growing on the edge of a dense willow thicket in full sun. There was a total of 14 individual stems in the clone, averaging 10.7 mature flowers per stem. Total number of mature flowers measured was 150.

CLONE B. Growing in a very wet location in the partial shade of a spruce-fir forest on the edge of a beaver pond about two miles northeast of the laboratory at 10,000 feet and collected on July 19. The average number of mature flowers was 3.1 on a total of 30 individual stems; 94 mature flowers were measured.

CLONE C. Chosen from a population in an aspen forest on laboratory property. The clone was collected on July 23 in a partially shaded rocky stream bed. This clone had 32 stems, the largest number of individual stems of the four clones. Average number of mature flowers per stem was 4.1; 132 mature flowers were measured from this clone.

CLONE D. Growing in a willow thicket near Copper Creek adjacent to the laboratory. The soil was wet and rocky, the clone growing in partial shade. Collection was on July 7. The three individual stems of this clone, all flowering, averaged 13.3 mature flowers per stem and totaled 40 mature flowers suitable for measurement.

DISCUSSION

The variation pattern for each of the four studied clones of *Mertensia ciliata* is striking enough that a given clump can be identified on the basis of a distinctive combination of average length of calyx, corolla-tube and corolla-limb (fig. 1). On the other hand, individual measurements within

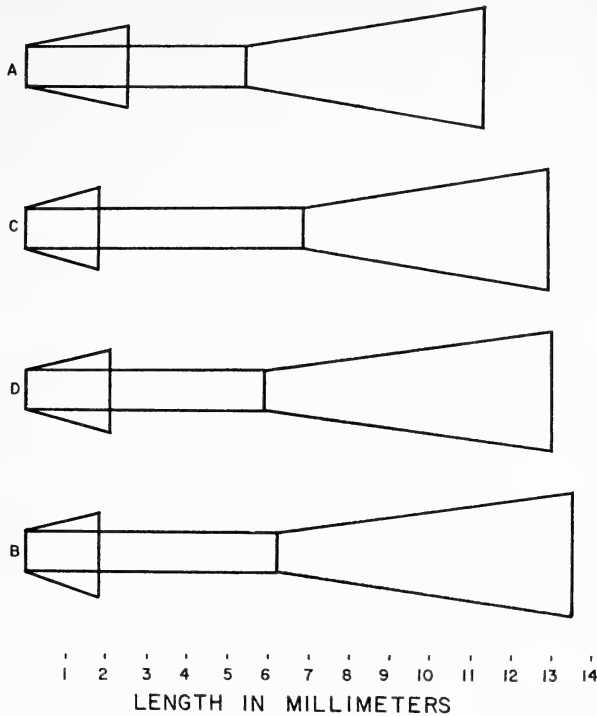


FIG. 1. Idiograms showing average lengths in millimeters of calyx, corolla tube, and corolla limb in clones A, B, C, and D of *Mertensia ciliata*.

each clone vary considerably for these three characteristics (fig. 2). However, the range of variation of a character in a clone usually does not overlap completely with that of the same character in other clones. These observed variations within and among the clones could be the result of three factors mentioned by Stebbins (1950): environmental modification, gene recombination, and mutation of genes or chromosomes. Considerations of the role of these factors as possible explanations for the variability observed is discussed in the following.

ENVIRONMENTAL MODIFICATIONS. Variability within a given clump should be a measure of environmental influences except for rare bud mutations or the unlikely possibility that one clump was derived from two or more seedlings. Floral characteristics were chosen for study because they are known to be frequently less easily influenced by environmental factors than are many vegetative characteristics (Clausen, Keck, and Hiesey, 1940; Anderson, 1929; Brainerd and Peitersen, 1920). All three characteristics vary considerably in range of measurements within each clone, such as the 1.5 mm. variation in Clone A calyx length which averages only 2.5 mm., the 3 mm. variation in corolla tube length in Clone

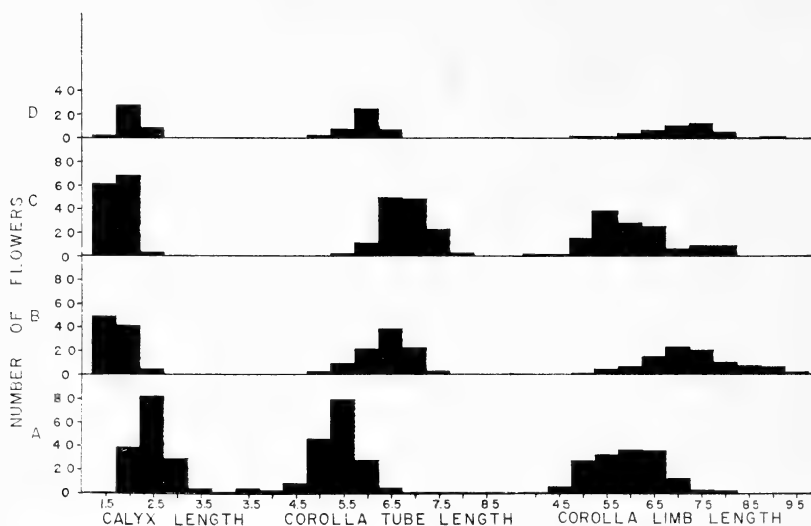


FIG. 2. Histograms showing distribution of individual measurements in millimeters of length of calyx, corolla tube, and corolla limb in clones A, B, C, and D of *Mertensia ciliata*.

A which averages 5.4 mm. in length, or the 4.5 mm. variation in corolla limb length for Clone B while average length is only 7.3 mm. This indicates that gene action, even in the fairly uniform environment of a single clone, differs in the final expression of length of calyx and corolla. To determine the various environmental factors that control the diverse action of these genes is difficult even in the imagination. External conditions such as soil, temperature, light, humidity, and biotic interactions would usually be expected to vary comparatively slightly during the development of the flower primordia of a single clump. Internal conditions such as amount and distance of the vascular supply, internal temperature, chemical environment, and the differing interaction of other genes in ontogeny would perhaps be more important than external environment since a slight variation of internal environment during the delicate interactions between gene initiation and the end result of expression could alter the phenotype. Whichever of the external or internal conditions may be important, their effect on the genes controlling calyx and corolla length accounts for a large proportion of the variation observed in this study, probably all of the intracolon variability. This would support the idea that corolla and calyx length in this case are quantitative characteristics, dependent on multiple genes, since quantitative characteristics are usually subject to considerable modification by environment (Srb and Owen, 1952).

GENE RECOMBINATION AND MUTATION. While the somatic variation discussed above cannot result in permanent changes in the species, gene

recombination and/or gene and chromosomal mutation are thought to contribute to variation that can foster evolutionary change in the species (Stebbins, 1950). Whether gene recombination and mutations could account for the differences among these four clones cannot be determined from the results of this study. Probably some of the observed differences among clones would be attributed to dissimilarities in external or internal environments of the four clones. It must be noted again, however, that floral characteristics are probably less subject to environmental modification than are other features of external morphology. Floral differences based on the pattern of average length of calyx, corolla-tube, and corolla-limb illustrate a distinctive combination in each clone (fig. 1). On close examination of the individuals compounded in these means it is found that only a few flowers approach the extremes of the large range of variation, and that standard deviations, given in Table I, are not large. Also, the histograms for each clone do not closely coincide with those for the other clones, although considerable overlapping does occur (fig. 2). These patterns of difference among the clones are probably the result of gene recombination, mutation because of its rarer occurrence being a less likely source. If *Mertensia ciliata* has a large number of genes active in regulating corolla length, such as the estimated twelve or more controlling corolla size in *Nicotiana* (Smith, 1937), it would be plausible to assume such recombination of the many genes in different individual plants or clones. Close linkage between the polygenes that determine quantitative characteristics, however, is often assumed to restrict the range of recombination of characteristics (Smith, 1944). Nevertheless, while somatic variation is doubtless the main factor in accounting for the variation within each clump, the characteristic variation patterns presented here for calyx and corolla length would imply some genetic differences among the clones, probably, as a result of gene recombination.

SUMMARY

Length of calyx, corolla-tube, and corolla-limb were measured for four widely separated clumps, presumably clones, of *Mertensia ciliata* that were collected from four differing and widely separated sites in Gunnison County, Colorado. Comparisons of calyx and corolla lengths were made within and among the four clones. The considerable variation of the three characteristics found within each of the clones is attributed to external and internal environmental factors, internal conditions probably being more important. Variation patterns among the clones differ enough to give each clone a distinctive combination of average lengths for the three characteristics. In most cases, the range of variation in calyx and corolla length within each clone does not completely coincide with that of the other clones. These differences in variation patterns imply some genetic differences among the clones, probably as a result of gene recombination.

Department of Botany,
Butler University, Indianapolis, Indiana

LITERATURE CITED

- ANDERSON, E. 1929. Variation in *Aster anomalus*. Ann. Missouri Bot. Gard. 16: 129-144.
- BRAINERD, E., and E. K. PEITERSEN. 1920. Blackberries of New England—their classification. Vermont Agr. Exp. Sta. Bull. No. 217. 84 pp.
- CLAUSEN, J., D. D. KECK and W. M. HIESEY. 1940. Experimental studies on the nature of species. I. The effect of varied environments on western North American plants. Carnegie Inst. Publ. No. 520. 452 pp.
- SMITH, H. H. 1937. Inheritance of corolla color in the cross *Nicotiana Langsdorffii* by *N. Sanderae*. The relation between genes affecting size and color in certain species of *Nicotiana*. Genetics 22:347-375.
- . 1944. Recent studies on inheritance of quantitative characters in plants. Bot. Rev. 10:349-382.
- SRB, A. M., and R. D. OWEN. 1952. General Genetics. W. H. Freeman and Co. San Francisco, Calif. 561 pp.
- STEBBINS, G. L., JR. 1950. Variation and evolution in plants. Columbia Univ. Press. 643 pp.
- WILLIAMS, L. O. 1937. A monograph of the genus *Mertensia* in North America. Ann. Missouri Bot. Gard. 24:17-159.

NEW COMBINATIONS IN ASTER

ROXANA S. FERRIS

Through an inadvertence the following new combinations were not legally made in the recent "Flora of the Marshes of California" by Herbert L. Mason.

ASTER OCCIDENTALIS var. **parishii** (Gray) Ferris, comb. nov. *A. fremontii* var. *parishii* Gray, Syn. Fl. N. Amer. 1 (2): 192. 1884.

ASTER OCCIDENTALIS var. **delectabilis** (H. M. Hall) Ferris, comb. nov. *A. delectabilis* H. M. Hall, Univ. Calif. Publ. Bot. 3:82. 1907.

Both of these varieties occur in California in the Sierra Nevada and in the mountains of southern California, and they reoccur in the San Pedro Mártir of northern Baja California, Mexico.

Dudley Herbarium, Stanford University,
Stanford, California.

NOTES AND NEWS

Some publications of interest follow:

Under the auspices of the *Gobierno del Estado de México, Dirección de Recursos Naturales* (Toluca) publications on the *Flora del Estado de México* have continued to appear. During 1958 Professor Maximino Martínez completed the *Flora Medicinal* as well as the treatment of the Cactaceae and some forty smaller families; Professor Eizi Matuda treated the Gramineae, Umbelliferae and the Compositae.

Drawings of British Plants, by Stella Ross-Craig. Part XI. Droseraceae—Ficoidaceae. 39 pls. 1958. 9s. 6d. G. Bell and Sons, Ltd. London. Part XII. Umbelliferae (1). 36 pls. 1958. 9s. 6d. 1958.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. *The Herbaria of the World*. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$4.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany
University of California, Berkeley 4, California



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 5

JANUARY, 1960

Contents

	PAGE
THE DISTRIBUTION OF DWARF MISTLETOES, ARCEUTHOBium, IN CALIFORNIA, <i>Job Kuijt</i>	129
NUCLEAR CYTOLOGY OF THE CALIFORNIA MOUSE-TAILS (MYOSURUS), <i>Donald E. Stone</i>	139
VARIATION IN SECTION TRIGONOPHYLLAE OF NICOTIANA, <i>Philip V. Wells</i>	148
STUDIES ON SECOTIACEOUS FUNGI VII. SECOTIUM AND NEOSECOTIUM, <i>Rolf Singer and Alexander H. Smith</i>	152
REVIEW: Adriance S. Foster and Ernest M. Gifford, Jr., <i>Comparative Morphology of Vascular Plants</i> (Sanford Tepfer)	158
NOTES AND NEWS	160

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$6.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—JOHN THOMAS,

Dudley Herbarium, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: Herbert G. Baker, Department of Botany, University of California, Berkeley, California. First Vice-president: Malcolm A. Nobs, Carnegie Institution of Washington, Stanford, California. Second Vice-president: Herbert F. Copeland, Sacramento City College, Sacramento, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: John Thomas, Dudley Herbarium, Stanford University, Stanford, California.

THE DISTRIBUTION OF DWARF MISTLETOES, ARCEUTHOBIUM, IN CALIFORNIA

JOB KUIJT

There has long been need of a more careful geographical study of the western dwarf mistletoes than has been available thus far. This paper attempts, first of all, to correct certain misconceptions which have been carried along in the relevant literature. Secondly, it represents an effort to bring up to date what is reliably known about the distribution of dwarf mistletoes in California. Finally, it tries to discover whether there is geographical evidence for the existence of host forms in *Arceuthobium campylopodum* Engelm.

The California distribution of dwarf mistletoes is indeed of crucial importance in geographical considerations in the genus as a whole. For it is in this state that the Pinaceae, a family embracing all known hosts of North American dwarf mistletoes, reaches a high level of diversity. The geographic peculiarities of the genus in California may thus contribute to the understanding of similar features elsewhere.

The lists and maps contain all Californian collections of *A. americanum* Nutt. ex Engelm. and *A. douglasii* Engelm. which I have been able to find in the herbaria of the University of California at Berkeley and Los Angeles (UC and LA, respectively), the California Academy of Sciences at San Francisco (CAS), the Dudley Herbarium of Stanford University (DS), the two herbaria at Claremont (POM and RSA), the Santa Barbara Museum of Natural History (SBM), and the United States Department of Agriculture Forest Pathology herbaria at Albuquerque (FPA) and Berkeley (FPB). Such an approach is at this time not feasible for *A. campylopodum*, as hundreds of collections of this species have been made in California. I have chosen instead to select a number of collections of this species to be recorded here. This selection has been carried out with two objectives in mind: firstly, to give as extensive a picture of the distribution of *A. campylopodum* in the state as possible; and secondly, to compare the geographic ranges of the supposed host forms of this species. Such a procedure does not give a reliable idea of frequency of occurrence. This would have been equally true, however, had all collections been taken into account, because some recreational areas are represented in herbaria by disproportionately large numbers of collections. This is true particularly for the Monterey Peninsula. In a similar way, the mistletoe on digger pine is much more accessible and much more in evidence than, for example, the same species on sugar pine, and therefore the former is present in herbaria in numbers exaggerating its relative frequency. I believe therefore that selection of specimens, when based on some acquaintance with the species as they occur in nature, in this way can give a somewhat more accurate idea of geographic distribution. I am also refraining from citing specimens

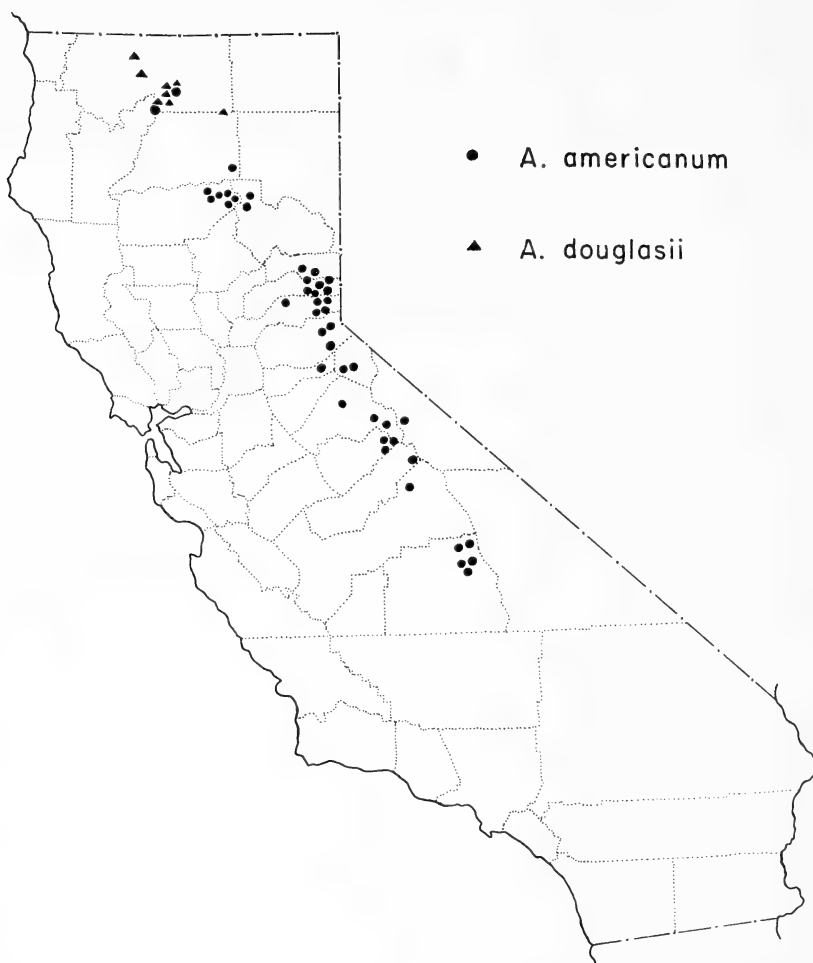


FIG. 1. Distribution of *Arceuthobium americanum* and *A. douglasii* in California.

which I have not personally seen. Especially in Gill (1935) some additional citations may be found which do not, however, modify the distributional patterns as here described, except where this author has repeated erroneous records from previous publications.

ARCEUTHOBIUM AMERICANUM Nutt. ex Engelm.

The lodgepole pine mistletoe is known from the boreal forests of the four western Canadian provinces and from all states west of the Rocky Mountains. It has been collected from a number of pines as well as from *Picea glauca* (Moench) Voss (Kuijt, 1955), but in California it is known from only *Pinus contorta*, *P. ponderosa*, and *P. jeffreyi* (see map, fig. 1).

On *Pinus contorta* Dougl. ex Loud.

TULARE COUNTY. North fork of Kern River, 2150 m., *Coville & Funston 1596* (DS); Bakeoven Meadows, 8100 ft., *Howell 27038* (CAS, DS, UC); ridge between Monache Meadows and Bakeoven Meadows, 8200 ft., *Munz 15220* (RSA); Funston Camp, Kern River Canyon, 6700 ft., *Peirson 1720* (RSA); Junction Meadows, Kern River, 8000 ft., *Raven 8349* (CAS, UC). FRESNO COUNTY. Huntington Lake, 7000 ft., *Solbrig 2420* (UC). MADERA COUNTY. Red's Meadows to Rainbow Falls, 7100 ft., *Raven 3678* (CAS, RSA). MARIPOSA COUNTY. Merced Lake trail, Yosemite National Park, *Schreiber 1948* (UC); Little Yosemite Valley, *Bolander 5095* (UC), *Rodin 877* (UC). TUOLUMNE COUNTY. Glen Aulin Camp, *Baldauf* (CAS); Morrison Creek, Mount Adams, *Braekett* (LA); YMCA camp, Pinecrest, 5500 ft., *Gill* (FPA). MONO COUNTY. 4.3 mi. west of Highway 120-395 junction, *Kuijt 1390* (UC). ALPINE COUNTY. Camp Wolfeforo, *Kuijt 1411* (UC); 0.5 mi. east of Grade Summit, *Kuijt 1412* (UC). AMADOR COUNTY. East of Lower Bear River Reservoir, *Quick 54-88* (CAS). EL DORADO COUNTY. Near Lily Lake, Glen Alpine Canyon, *Abrams 12753* (DS, RSA, UC); 16 mi. south of Tahoe City, *Kuijt 1335* (UC); Highway 50 at Pyramid Creek, *Kuijt 1513* (UC). PLACER COUNTY. 8.5 mi. west of Soda Springs, *Kuijt 1330* (UC); 10 mi. north of Tahoe City on Highway 89, *Kuijt 1331* (UC); 3.5 mi. north of Tahoe City on Highway 89, *Kuijt 1332* (UC); Tahoe Meadow, *Schreiber 776* (UC). NEVADA COUNTY. Near Donner Lake, *Dudley* (DS); Mayen's Meadow, near Truckee, *Sonne* (UC); Trout Creek near Truckee, *Thomson* (CAS); Truckee, 6300 ft. (FPA); Hobart Mills (FPA). SIERRA COUNTY. 9.5 mi. north of Truckee, *Kuijt 1344* (UC); Salmon Lake, *Sutcliffe* (CAS); Gold Lake (FPA). PLUMAS COUNTY. 18 mi. north of Greenville on Highway 89, *Kuijt 1350* (UC); Gold Lake, *Mason 1079* (UC). TEHAMA COUNTY. 7 mi. west of Highway 36-89 junction at Lake Almanor, *Kuijt 1352* (UC); 13 mi. west of Highway 36-89 junction at Lake Almanor, *Kuijt 1354* (UC); near Ranger Station, Mineral Campgrounds, *Kuijt 1358* (UC); along Deer Creek, 1.5 mi. south of Highway 32-36 junction, *Kuijt 1501* (UC); Spring camp near Childs Meadow, *Quick 53-129* (CAS). SHASTA COUNTY. Thousand Lake Basin, 6400 ft., *Peirson 10136* (RSA). SISKIYOU COUNTY. Military Pass, Mount Shasta, *Cooke 16034* (DS, UC); north fork, Sacramento River, 6600 ft., *Raven 10456* (CAS).

On *Pinus jeffreyi* Grev. & Balf.

PLACER COUNTY. 9.2 mi. north of Tahoe City on Highway 89, *Kuijt 1343* (UC).

On *Pinus ponderosa* Dougl. ex Laws.

TEHAMA COUNTY. 13 mi. west of Highway 36-89 junction at Lake Almanor, *Kuijt 1355* (UC).

DISCUSSION. California represents one of the two southernmost extensions of the lodgepole pine mistletoe, the other being in the Rocky Mountain area of Colorado. From a comparison of Figure 1 with the known distribution of *Pinus contorta* (Critchfield, 1957, fig. 26), it is evident that at least in California the geographic range of the lodgepole pine mistletoe corresponds rather closely to that of its most common host. The exceptions to this rule are seen in the isolated and apparently healthy populations of lodgepole pine in the San Bernardino and San Jacinto mountains, California, and in Baja California, Mexico, and of *P. contorta* subsp. *bolanderi* (Parl.) Critchf. on the Mendocino coast of California. It is also notable that the subsp. *contorta*, although in direct contact with subsp. *murrayana* (Balf.) Critchf. in northern California, has not yet been reported as host for *Arceuthobium americanum*. Indeed this appears

to be true outside the state, as I have seen no record of *A. americanum* anywhere in the range of *Pinus contorta* subsp. *contorta* (Kuijt, 1956). This is more likely to be a case of ecological or spatial isolation than resistance on the part of the host, as various other species of pine and even a spruce may be parasitized by *Arceuthobium americanum*. Furthermore, all subspecies of *Pinus contorta* are susceptible to *Arceuthobium campylopodum* in one or more localities.

It is a remarkable fact that *A. americanum* appears to be unable to perpetuate itself for long periods of time in stands of *Pinus jeffreyi* and *P. ponderosa*. Wherever infected individuals of these hosts are found, infected lodgepole pine is nearby and almost surely is the source of the former infections. This is the more remarkable because the brooming induced on Jeffrey and ponderosa pine is almost identical to that on lodgepole pine (Kuijt, 1958). There are factors quite apart from sympatotomy, therefore, which distinguish the spread of this species of dwarf mistletoe in stands of various pine species. Whether these factors are climatological, or whether in Jeffrey and ponderosa pine there is a greater percentage of resistant trees, is impossible to say at present.

ARCEUTHOBIUM CAMPYLOPODUM Engelm.

This species is the most abundant one in California (see map, fig. 2). Outside the state it is found from Alaska and British Columbia, largely west of the Rocky Mountains, to the Mexican border (and across into Baja California). It parasitizes species of *Abies*, *Larix*, *Pinus*, *Picea*, and *Tsuga*. All but *Larix* have been reported as hosts for *Arceuthobium campylopodum* in California, but in greatly different frequencies.

I have attempted, both in the listing and mapping of the specimens selected for my purpose, to group herbarium specimens according to the affinities of their hosts. In this way I have used the following host categories as criteria for division: *Abies*; *Picea*; *Tsuga*; and the three main subdivisions of *Pinus*, namely, the yellow, white, and pinyon pines. I want to make clear that such a subdivision is not based on my acceptance of the corresponding host forms as recognized by Gill (1935), but rather is an effort to test their validity.

On *Abies*.

TULARE COUNTY. Cone Peak Camp, Kaweah and Kings River, *Dudley* (DS); between Junction Meadows and the hot springs, 7500 ft., *Raven* 8381 (CAS). FRESNO COUNTY. Charlotte Creek, Bubbs Creek, *Howell* 15674 (CAS); 2 mi. south of summit of Shaver Lake-Dinkey Creek road, *Quick* 53-27 (CAS); Huntington Lake, 7000 ft., *Wall* 67 (CAS). TUOLUMNE COUNTY. Southeast of Strawberry Lake, 6500-7200 ft., *Quick* 1734 (CAS); southeast of Pinecrest, *Quick* 50-40 (CAS); Tuolumne Canyon, *Clemens* (CAS). AMADOR COUNTY. East of Lower Bear Reservoir, *Quick* 54-87 (CAS). ALPINE COUNTY. Silver Creek, east side of Ebbetts Pass, 6800 ft., *Howitt* (CAS). EL DORADO COUNTY. Near north end of Echo Lake, *Howell* 22902 (CAS); near Camino, *Kuijt* 1272 (UC); Tehoma, Lake Tahoe, *Kuijt* 1340 (UC). PLACER COUNTY. Trail to Mount Ellis above Homewood, *Schreiber* 891 (UC). NEVADA COUNTY. Baltic Trail, *Dudley* (DS). PLUMAS COUNTY. Taylorsville, *Clemens* (CAS); 8 mi. north of Greenville, *Kuijt* 1349 (UC). BUTTE COUNTY. Jonesville, 1600 m.,

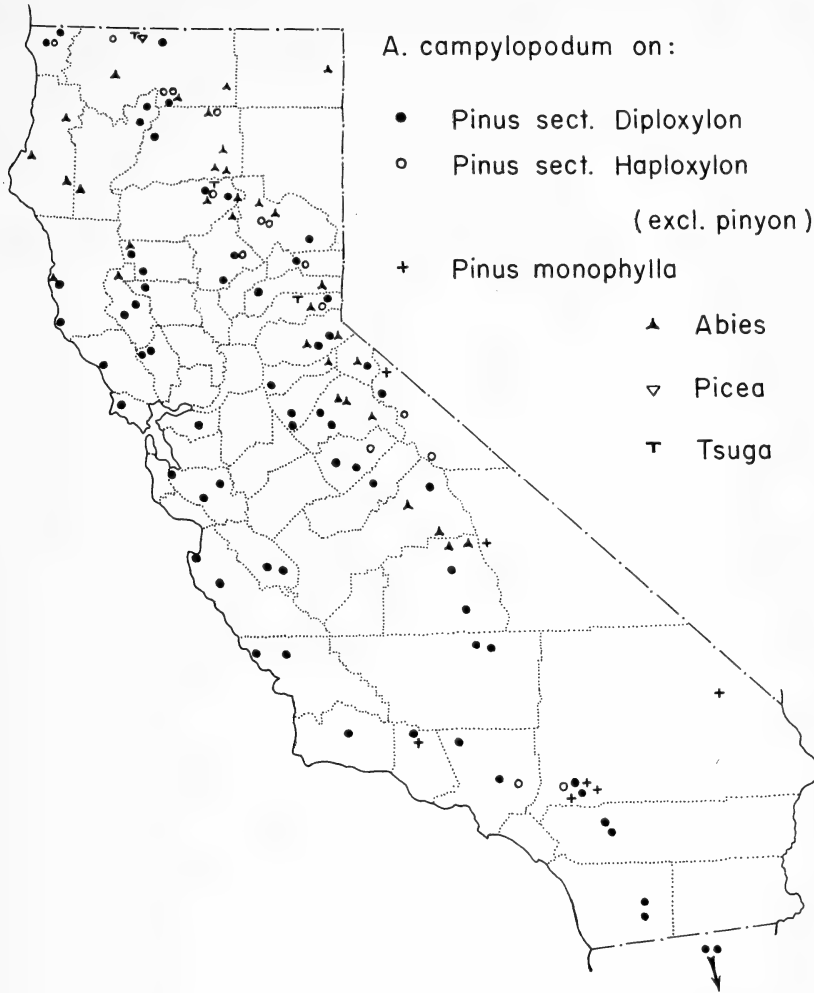


FIG. 2. Distribution of *Arceuthobium campylopodum* in California.

Copeland (CAS). TEHAMA COUNTY. 11 mi. west of Highway 36-89 junction at Lake Almanor, *Kuijt* 1353 (UC); 5 mi. west of Mineral, *Kuijt* 1359 (UC). SHASTA COUNTY. Highway 89 at Pondosa junction, *Kuijt* 1368 (UC); 1.5 mi. east of Viola, *Kuijt* 1364 (UC). LASSEN COUNTY. 1 mi. below Drakesbad, Mount Lassen, 5400 ft., *Cain* 114 (DS); Crater Mountain, ca. 15 mi. west of Eagle Lake, 7300 ft., *Whitney* 1703 (UC); MODOC COUNTY. Campgrounds at Cedar Pass, Warner Mountains, *Alava* (UC). SISKIYOU COUNTY. East of Bartle, at border of Modoc National Forest, *Newcomb* 156 (UC); Sisson southern trail, Mount Shasta, *Cooke* 13574 (DS); summit of Cayenne Ridge, near Marble Mountain, *Ownbey* 2212 (CAS, DS). HUMBOLDT COUNTY. Lasseck's Peaks, between Goat Camp and Signal Peak, *Kildale* 2634 (DS); ridges east of Corral Prairie, Trinity Summit, *Tracy* 10571 (UC); Eureka, *Tracy* 3984 (UC). TRINITY COUNTY. South Fork Mountain, *Parks & Tracy* (UC). MENDOCINO COUNTY. Van Damme State Park, *Kuijt* 1216 (UC). GLENN COUNTY. Plaskett Meadows, 6000 ft., *Howell* 19283 (CAS). LAKE COUNTY. *Mackie* (UC): see the discussion under *A. douglasii*.

On *Picea breweriana* Wats.

SISKIYOU COUNTY. Ridge above Applegate Creek, Dry Lake Lookout, 6500 ft., *Meinecke* (FPB).

On *Tsuga mertensiana* (Bong.) Carr.

PLACER COUNTY. Emigrant Gap, *Jones* (POM). TEHAMA COUNTY. Mineral, 6300 ft., *Long* (FPB). SISKIYOU COUNTY. Along head of Applegate Creek, north side of pass to Fort Gough, 6000 ft., *Meinecke* (FPB).

On Yellow Pines. (*Pinus* sect. *Diploxylon*: *P. attenuata* Lemmon, *P. contorta*, *P. jeffreyi*, *P. ponderosa*, *P. coulteri* Don, *P. sabiniana* Dougl. ex Don, *P. radiata* Don, *P. muricata* Don.)

BAJA CALIFORNIA, MEXICO:¹ Low hills northwest of La Encantada, Sierra San Pedro Mártir, 7300–7400 ft., *Wiggins & Demaree 5018* (DS, UC, LA); “San Pedro Mártir”, *Brandegee* (UC). CALIFORNIA: SAN DIEGO COUNTY. Pine Hills, near Julian, ca. 4250 ft., *Brown* (RSA); base of Stonewall Peak, *Wiggins 2725* (DS). RIVERSIDE COUNTY. Idyllwild-Banning, *Clokey & Anderson 6574* (RSA, UC); south side of San Jacinto Mountains, 5400 ft., *Hall 2616* (UC). SAN BERNARDINO COUNTY. Mill Creek, *Smith 15A* (UC); Lake Arrowhead, *MacFadden 14737* (CAS). LOS ANGELES COUNTY. Elizabeth Lake Canyon, Liebre Mountains, *Dudley & Lamb 4411* (DS); Pine Flats, 20 mi. north of Sierra Madre, Angeles N.F., 6000 ft., *Sloan* (FPB). VENTURA COUNTY. Mount Pinos, *Hall 6642* (UC). SANTA BARRERA COUNTY. Figueroa Mountain, *Pollard* (CAS). KERN COUNTY. Near Havilah, 900 m., *Coville & Funston 1073* (DS); 4 mi. west of Kernville, 4000 ft., *Gould 1010* (DS). SAN LUIS OBISPO COUNTY. Cambria, *Hoover 6448* (CAS); Santa Margarita, *Mason 525* (UC); near Paso Robles, *Summers 926* (UC). TULARE COUNTY. Near Mineral King, 2700 m., *Coville & Funston 1460* (DS); Peppermint Valley, *Dudley* (DS). FRESNO COUNTY. Vermillion Valley, 7700 ft., *Raven 5825* (CAS). SAN BENITO COUNTY. On ridge above New Idria reservoir, *Kuijt 1310* (UC); on road to New Idria, 4.5 mi. south of Bitterwater junction, *Kuijt 1300* (UC). MONTEREY COUNTY. Pacific Grove, *Coleman* (DS); Millers Canyon, Santa Lucia Mountains, 4300 ft., *Ferris 12158* (DS). SANTA CLARA COUNTY. Loma Prieta, *Dudley* (DS); slopes of Mount Umunhun, *Ferris 2083* (DS); Arboretum, Stanford University, *Long* (DS).² CONTRA COSTA COUNTY. Mount Diablo, *Abrams 4356* (DS). MADERA COUNTY. Ca. 9 mi. west of Oakhurst, *Kuijt 1254* (UC). MARIPOSA COUNTY. Ca. 3 mi. west of Mount Bullion, *Kuijt 1253* (UC); on road to Wawona, *Jussell 13* (UC). TUOLUMNE COUNTY. Cottonwood Meadows, east of Mather, *Clausen 1777* (DS); near Pinecrest, *Quick 55–46* (CAS). CALAVERAS COUNTY. West of Stanislaus River on road from Vallecito to Columbia, *Quick 53–141* (CAS); 1.5 mi. east of Copperopolis on Highway 4, *Kuijt 1410* (UC). AMADOR COUNTY. On road to Buena Vista, ca. 1 mi. south of Ione, 400 ft., *Newcomb* (UC). MONO COUNTY. 3 mi. east of Sonora Pass, *Kuijt 1432* (UC). ALPINE COUNTY. Silver Creek Public Camp, *Munz 21347* (RSA). EL DORADO COUNTY. Lily Lake, Glen Alpine Canyon, *Abrams 12752* (DS); near Camino, *Kuijt 1273* (UC). PLACER COUNTY. 1 mi. north of Tahoe City on Highway 89, *Kuijt 1333* (UC). NEVADA COUNTY. Spenceville, *Eastwood 3420* (CAS). SIERRA COUNTY. Gold Lake, *Barker 254* (DS). BUTTE COUNTY. Hills near Big Chico Creek, east of Chico, *Heller 11144* (DS); Bangor, *Rose* (CAS). PLUMAS COUNTY. 21.5 mi. north of Sierraville, *Kuijt 1346* (UC). SHASTA COUNTY. Near Morleys, *Baker* (UC). SISKIYOU COUNTY. Sisson southern trail, Mount Shasta, *Cooke 11593* (CAS, DS, UC); west of Craggy Mountain, northwest of Yreka,

¹ As far as I can ascertain, these are the only Mexican records of *A. campylopodum*. The species *A. vaginalum*, which is not known from California or Baja California, does occur in areas of non-peninsular Mexico.

² Introduced into the Arboretum at an early date, since the mistletoe was already there at the turn of the century (Peirce, 1905).

Ownbey & Brown 2425 (UC). DEL NORTE COUNTY. Gasquet Mountain, *Eastwood 12138* (CAS); Elk Camp Ridge, *Parks 24063* (UC). TRINITY COUNTY. Near Scott Ranch, *Cantelow 1659* (RSA); near Trinity Center, *Howell 12790* (CAS). TEHAMA COUNTY. 15 mi. west of Highway 36-89 junction at Lake Almanor, *Kuijt 1357* (UC); Manton, *Kuijt 1362* (UC). MENDOCINO COUNTY. Pygmy forest above Van Damme State Park, *Kuijt 1215* (UC); Point Arena, *Mason 7168* (UC). GLENN COUNTY. .5 mi. above Long Point Fire Lookout Station, 3750 ft., *Newcomb 148* (UC); 2.1 mi. north of Stonyford, *Kuijt 1506* (UC). LAKE COUNTY. Kelseyville, *Jussell* (CAS); near Lucerne, *Sutcliffe* (CAS). COLUSA COUNTY. Stonyford-Upper Lake road, below Old Mill Campgrounds, 3700 ft., *Newcomb 146* (UC). NAPA COUNTY. Mount St. Helena, *Howell 2204* (CAS); 3 mi. from Aetna Springs on Butts Canyon Road to Middletown, *Howell 5618* (CAS). SONOMA COUNTY. Fort Ross, *Mason 4285* (UC). MARIN COUNTY. Inverness Ridge, *Howell 19686* (CAS).

On *Pinus monophylla* Torr. & Frém.

SAN BERNARDINO COUNTY. East slope of Providence Mountains, *Munz, Johnston & Harwood 4272* (POM); north slope of San Bernardino Mountains, *Parish & Parish 1442* (DS, UC); Arrastre Creek, 3 mi. southeast of Baldwin Lake, 6700 ft., *Jaeger* (POM); 5 mi. southeast of Ivanpah, *Gill & Wright* (DS). VENTURA COUNTY. Seymour Creek, Mount Pinos, 6000 ft., *Peirson 3251* (POM, RSA). INYO COUNTY. Ca. 3 mi. west of Lone Pine on Mount Whitney road, *Kuijt 1389* (UC). MONO COUNTY. 6 mi. south of Coleville, *Kuijt 1413* (UC).

On white pines, excluding pinyon (*Pinus* sect. *Haploxylon*, excl. pinyon: *P. albicaulis* Engelm., *P. lambertiana* Dougl., *P. flexilis* James, and *P. monticola* Dougl. ex Don).

SAN BERNARDINO COUNTY. West slope, Job's Peak, 5000 ft., on *P. lambertiana*, *Ewan 3564* (POM, DS, UC). LOS ANGELES COUNTY. Between Wrightwood and Kratka Ridge, Angeles N.F., on *P. lambertiana*, *Embree* (UC). MARIPOSA COUNTY. Fish Camp Creek, on *P. lambertiana*, *Hedgecock and Meinecke* (UC). MONO COUNTY. On saddle above Convict Lake, 8800 ft., on *P. flexilis*, *Kuijt 1415* (UC); 2 mi. southeast of Lundy Lake, on *P. (?) flexilis*, *Hendrix 616* (UC). PLACER COUNTY. Near Summit, Tahoe N.F., 7500 ft., on *P. monticola*, *Wagner* (FPB). SIERRA COUNTY. Between Downieville and Forest, 5000 ft., on *P. lambertiana*, *Boyce* (FPB). BUTTE COUNTY. Big Bar Mountain ridge east of Pulga, on *P. lambertiana*, *Quick 53-32*. PLUMAS COUNTY. Southeast of Meadow Valley, on *P. lambertiana*, *Quick 53-120* (CAS); Meadow Valley, on *P. lambertiana*, *Weatherby 1667* (UC). TEHAMA COUNTY. 2 mi. north of Hole-in-Ground Campgrounds, on *P. lambertiana*, *Kuijt 1502* (UC). SHASTA COUNTY. Highway 89 at Pondosa junction, on *P. lambertiana*, *Kuijt 1369* (UC). SISKIYOU COUNTY. North slope of Shastina, on *P. albicaulis*, *Cooke 11576* (DS); west fork of Molly Creek, on *P. albicaulis*, *Butler 272* (UC); head of Applegate Creek, 5800 ft., *Wagner* (FPB). DEL NORTE COUNTY. Gordon Mountain, 4100 ft., on *P. monticola*, *Newcomb 165* (UC).

DISCUSSION. All major areas of yellow pine in California are infected by *A. campylopodum*. This conclusion cannot be avoided when the specimens cited above are considered. There are, however, differences in the frequency of *A. campylopodum* which are not evident from this enumeration. Such differences are difficult to measure, but are nevertheless recognizable in the field.

The only California yellow pine which appears to be free of this mistletoe is *P. torreyana* Parry ex Carr. I have searched for the parasite in the Del Mar area without success, and I have never seen a herbarium specimen with this pine as host. The spatial isolation of this pine from its fellow

species would lead one to conclude that its health is not a question of immunity, but rather that isolation from other pines has, at the same time, kept *Arceuthobium* from reaching the Torrey pine.³ I am currently germinating *A. campylopodum* on some seedlings of this pine, but cannot as yet report on it.⁴

Infected white pines have been collected a great deal less frequently than yellow pines. This is of course partly due to their comparative rarity in the state, especially *P. albicaulis*, *P. flexilis*, and *P. monticola*. *Pinus balfouriana* Grev. & Balf. has also been reported as host from Black Butte, Siskiyou County (Gill, 1935). The latter author also makes reference to a supposed host record of California *P. aristata* Engelm. by Garrett (1921) which, however, is erroneous, as Garrett reports this host only from Bryce Canyon, Utah.

The sugar pine I believe is more frequently infected than the record indicates, and this discrepancy is probably due to the inaccessibility of infections on this tree. It is nevertheless true, as Gill (1935) pointed out, that infected trees of this pine are fairly infrequent and are usually associated with other infected members of the Pinaceae.

The pinyon pines have an even more spotty collection record. This situation indeed is evident in the field since infected trees are rare and appear to occur in small groups. The interesting fact is that such a small number of collections (these are all the pinyon records I have found from California) should be so widely spaced. I have heard it said that the pinyon pine mistletoe is equally spotty in its occurrence outside California.

As far as *Abies* is concerned, it seems to be fairly commonly infected in northern California. The incomplete record for some counties in the Sierra Nevada I suspect to be due to an infrequency of collecting rather than to a rarity of occurrence. This can be checked only by further collections, however. The notable fact in this host genus is that the geographically most isolated fir, *Abies bracteata* (Don) Poit., is free of dwarf mistletoe. Do we here have a parallel to the situation seen in *Pinus torreyana*? Is the lack of infection of *Abies bracteata* due to immunity, or to isolation from dwarf mistletoe? Cross-inoculations may well supply the answer to this question. It is an interesting fact that within a few miles of the *Abies bracteata* populations in the Santa Lucia Mountains the Coulter pine is heavily infected with *Arceuthobium campylopodum*.

There remain to be considered, finally, the only California records known of *A. campylopodum* on *Picea* and *Tsuga*. The small number of

³ Dr. H. L. Mason reports that the pines of Santa Cruz Island are apparently free of mistletoe.

⁴ Since writing the above, the inoculations have been inspected and found successful. The source of the mistletoe seed was Mount Diablo where the dwarf mistletoe grows indiscriminately on both *Pinus coulteri* and *P. sabiniana*. Seeds were placed individually in axils of leaves and fascicles of seedlings of *P. torreyana* (from Del Mar) less than a year of age, on November 6, 1957. At present (January, 1960) a large number of mistletoe shoots are present and one pine has died, perhaps as a result of heavy infection.

collections of these conifers as hosts, and the distances between their localities of origin, would certainly militate against basing host forms upon these genera. The three isolated collections on Mountain Hemlock are significant in this respect, but the infected *Picea breweriana* in Siskiyou County is an even better case in point. According to Gill (1935), the nearest known infected spruces are from Idaho and Arizona!

How then does the geographical evidence bear upon the status of the host forms of *Arceuthobium campylopodum*? It is quite clear that it does not, in itself, support the notion. The host forms considered by Gill as "minor" forms [f. *cyanocarpum* (Nelson) Gill, f. *blumeri* (Nelson) Gill, and f. *microcarpum* (Englm.) Gill] are found within the areas occupied by even a single "major" form, f. *campylopodum*. In fact, f. *campylopodum* is known from practically every county where any of the other forms have been collected. Gill admits that his three "minor" forms are found only in association with other infected species. In California, at least, the host forms do not have geographic independence. These facts alone, of course, do not preclude racial differentiation as to hosts.

It is a common field experience to find a heavily infected species of one tree together with another species, apparently healthy here, but infected elsewhere. This puzzling situation is frequently observed in mixed fir and pine stands of the Sierra Nevada and elsewhere. It seems to me that such situations more than any other considerations have led to the supposition of host forms. In my opinion the taxonomic recognition of such host forms ignores two important possibilities. First of all, it fails to take into account a possible variation in susceptibility even *within* a host species. Secondly, it largely ignores those isolated but significant instances where, for example, a lodgepole pine has become infected obviously from the heavily infected fir towering above it. When geographic data are thus considered together with the results of the past cross-inoculations (Weir, 1918) and natural apparent transfers between *Pinus*, *Picea*, *Abies*, *Larix*, and *Tsuga* (Kuijt, 1955) it becomes evident that the host forms are not natural groups and are, indeed, misleading. The species *A. campylopodum* cannot, in my opinion, be subdivided into natural groups until more is known about the resistance differences (if any) both between and within host species.

ARCEUTHOBIMUM DOUGLASII Engelm.

The Douglas fir mistletoe is the rarest of California dwarf mistletoes (see map, fig. 1). Its range outside the state shows similarities to that of *A. americanum*. It is found from southern British Columbia to California and Arizona and New Mexico. It is not known from the coastal areas of the Pacific Northwest, even where the Douglas fir reaches its maximum development. It rarely grows on anything but Douglas fir (*Pseudotsuga menziesii*), the only known host from California.

On *Pseudotsuga menziesii* (Mirb.) Franco.

SHASTA COUNTY. Highway 89 at Pondosa junction, 4000 ft., *Kuijt 1367* (UC).
SISKIYOU COUNTY. Southwest slopes of Mount Shasta, 5000 ft., *Cooke 13920* (LA);

north side of Cascade Gulch, Mount Shasta, 5000 ft., *Cooke 17729* (CAS); near Upton, Mount Shasta, 4000 ft., *Hall & Babcock 4078* (UC); 1 mi. east of Highway 89-99 junction, *Kuijt 1371* (UC); road to Gumboot Lake, south fork of Sacramento River, west of Shasta, 4500 ft., *Smith & Bacigalupe* (UC); west fork of Cottonwood Creek, Siskiyou Mountains, *Wheeler 2783* (CAS, POM, LA); 2 mi. below Dry Lake Lookout, Oak Knoll Ranger Station, 5000 ft., *Gill* (FPA).

DISCUSSION. So much confusion exists as to this species in California that it is necessary first to make a few corrections.

To begin with, there is the question of Jepson's (1923) reference to *Arceuthobium douglasii* on *Pseudotsuga macrocarpa* (Vasey) Mayr in southern California. As far as I can discover there is no voucher for this suggestion in the Jepson Herbarium or in the University of California Herbarium at Berkeley, or elsewhere. In Jepson's field notebooks there is no mention of *Arceuthobium douglasii*. Whatever the statement was originally based on, at present the record is unacceptable.

A second source of confusion has been Jepson's (1914) misquotation of Engelmann (1880). In this work, Engelmann refers to *A. douglasii* var. *abietinum* Engelm. as occurring on *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. in Sierra Valley, Sierra County. Jepson, however, simply repeats this locality for *Arceuthobium douglasii*, and this error is perpetuated by Gill (1935). The var. *abietinum* is undoubtedly referable to *A. campylopodum*, as are the early *A. douglasii* var. *laricis* and var. *tsugense*. There is no reliable record of *A. douglasii* (in the modern sense) from Sierra County.

A third error was first introduced by Jepson (1923) and again repeated by Gill (1935). It concerns a specimen collected by Mackie, "Lake Co., Aug. 1902, on *Pseudotsuga taxifolia*." Both Jepson and Gill refer to *Arceuthobium douglasii* in Lake County. Gill's reference is based on the Mackie collection, and Jepson's probably also. The specimen in question (UC 54672) includes some fragmented material, a couple of infected branches of *Abies* sp. [probably *A. grandis* (Dougl. ex Don) Lindl.], and a cone of *Pseudotsuga menziesii*. I have no doubt, both because of the flowering condition of the plants and because of their large size, that the collection is *Arceuthobium campylopodum*, and that the Douglas fir cone was included by mistake.

As it stands, then, *A. douglasii* is known only from the northern part of the state. In fact, the only known collection outside Siskiyou County was made within half a mile of the county line. There is in this species a most striking discrepancy between the geographic ranges of host and parasite. The common Douglas fir may be found in the Coast Ranges as far south as the Santa Lucia Mountains, and in the Sierra Nevada as far south as Big Creek (San Joaquin River), Fresno County. The dwarf mistletoe, almost exclusively restricted to this tree, somehow has not been able to invade large portions of its host's range. Whether these extensive areas of Douglas fir have remained healthy because of spatial isolation, resistance, or climatic barriers, or whether differences in forest composition here play

a decisive role in limiting the spread of *A. douglasii*, are questions which remain to be clarified.

Department of Biology and Botany,
University of British Columbia,
Vancouver, Canada

LITERATURE CITED

- CRITCHFIELD, W. B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Found. Publ. No. 3.
- ENGELMANN, G. 1880. In Watson, S. Botany of California, 2:106-107.
- GARRETT, A. O. 1921. Forest tree diseases. Trans. Utah Acad. Sci. 2:182-189.
- GILL, L. S. 1935. *Arceuthobium* in the United States. Trans. Conn. Acad. Arts & Sci. 32:111-245.
- JEPSON, W. L. 1914. A flora of California. San Francisco.
- . 1923. A manual of the flowering plants of California. Berkeley.
- KUIJT, JOB. 1955. Dwarf mistletoes. Bot. Rev. 21:569-628.
- . 1956. A new record of dwarf mistletoe on lodgepole and western white pine. Madroño 13:170-172.
- . 1958. Morphological aspects of parasitism in the dwarf mistletoes (*Arceuthobium*). Dissertation, Univ. Calif., Berkeley.
- PEIRCE, G. J. 1905. The dissemination and germination of *Arceuthobium occidentale* Eng. Ann. Bot. 19:99-113.
- WEIR, J. R. 1918. Experimental investigation on the genus *Razoumofskyia*. Bot. Gaz. 66:1-31.

NUCLEAR CYTOLOGY OF THE CALIFORNIA MOUSE-TAILS (MYOSURUS)¹

DONALD E. STONE

INTRODUCTION

Published accounts of the chromosome numbers in the genus *Myosurus* are limited to three brief reports concerned exclusively with European representatives. In the 1945 edition of the "Chromosome Atlas," a single citation (Gregory, 1941) noted the chromosome number of *M. minimus* as $n=8$. A check of Gregory's paper, however, reveals that *Myosurus* was one of the few genera in the family for which he had no first hand information. Instead, his citation is based upon the work of Mann (1892) and Hocquette (1922), who found $n=8$ and $2n=16$ respectively. The haploid number was published by Mann as a footnote to his figure 5: "Monaster stage of archesporium, with 8 chromatin segments." Hocquette's account was likewise lacking in details, as his study was part of a general survey of the Ranunculaceae.

The third reference to original work is in the 1955 edition of the "Chromosome Atlas." It is of interest to note that here the earlier citations of Mann and Hocquette are dropped in favor of a more recent

¹ Part of a dissertation submitted to the University of California at Berkeley as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

count by Ehrenberg (1945). Working on Swedish material, Ehrenberg found about 28 chromosomes in the somatic cells. His counts of nine cells showed variations of from 27 to 30 chromosomes, with the best three slides having 28, 28 and 29. He suggests that the Swedish material is tetraploid, being derived from a diploid race with a base number of 7. Hocquette's report of a haploid number of 8 is considered to offer little difficulty as the

TABLE 1. MYOSURUS SPECIMENS CYTOLOGICALLY EXAMINED AND DOCUMENTED.¹

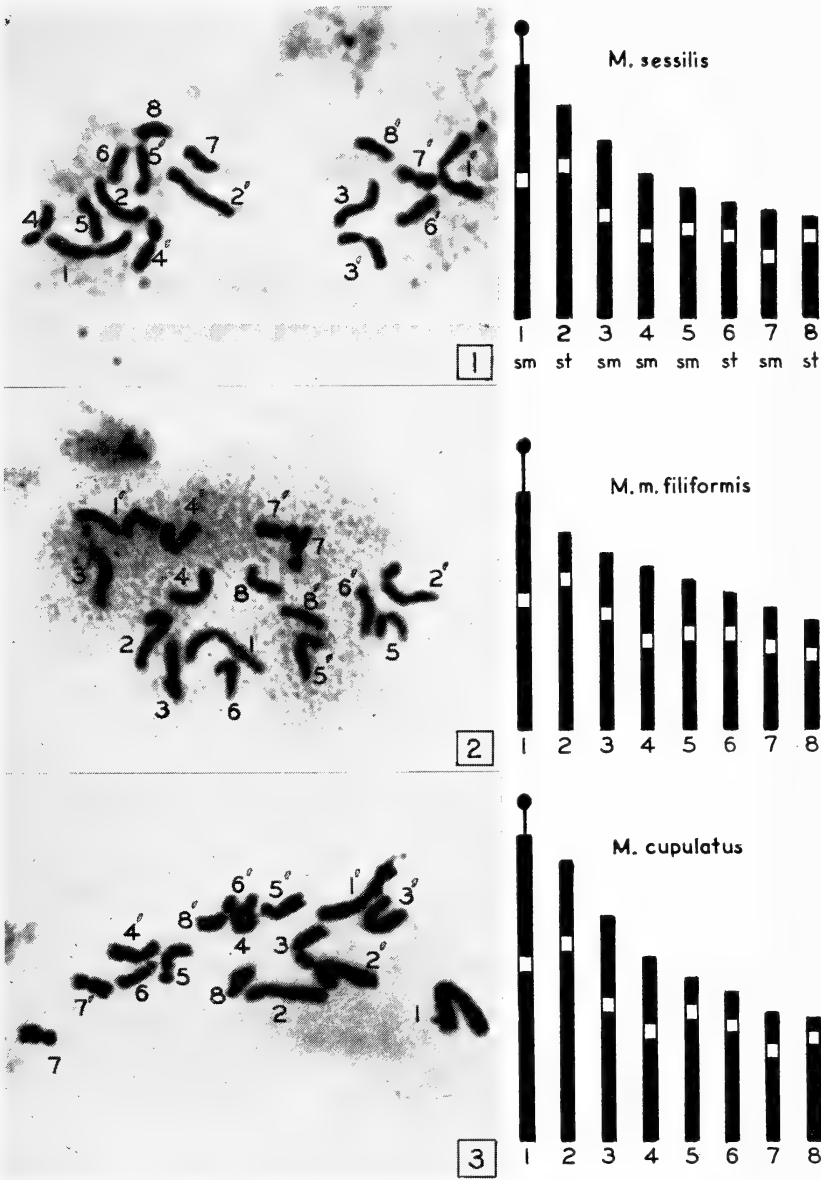
Collection Data	N	2N	Fig.
<i>M. sessilis</i> Watson			
Stone 1(14): 5 April 1953, 3 miles east of Maxwell on the Maxwell Road, Colusa County.*		16	1
Stone 1(10): same data as above.	8		4 & 5
<i>M. sessilis</i> subsp. <i>alopecuroides</i> (Greene) Stone			
Stone 7(22): 10 April 1953, same locality as above.	8	16	—
			6 & 7
<i>M. minimus</i> subsp. <i>apus</i> (Greene) Campbell			
Stone 5(1): 10 April 1953, Manning Flat, 5½ miles west of Lower Lake on the road to Kelseyville, Lake County	8		8
Stone 5(2): same data as above.	8		9
H. L. Mason 14275(2): 26 April 1952, 5 miles northeast of Crows Landing on the Crows Landing Road, Stanislaus County.		16	—
<i>M. minimus</i> L.			
J. Lid, Stone 73(1): 21 June 1955, Hud Island Vestfold County, Norway.		16	11
Stone 3(5): 4 April 1953, Manning Flat, 5½ miles west of Lower Lake on the road to Kelseyville, Lake County.	8		10
H. L. Mason 14501(4): 2 April 1953, 3 miles east of Hanford on the road to Visalia, Kings County.	8		—
<i>M. minimus</i> var. <i>filiformis</i> Greene			
Stone 7(13): 10 April 1953, 3 miles east of Maxwell on the Maxwell Road, Colusa County.		16	2
Stone 9(2): Spring, 1953, Ajax Field in Willows, Glenn County.	8		12-14
<i>M. aristatus</i> subsp. <i>montanus</i> (Campbell) Stone			
R. Bacigalupi 4238, Stone 15(5): April, 1953, Big Bear Lake, San Bernardino County.	8	16	—
			15
<i>M. cupulatus</i> Watson.			
T. Robbins 3480, Stone 17 (1): 29 April 1952, Providence Mountains, San Bernardino County.	8		16
		16	3

¹ Specimens documenting the chromosome counts have been deposited in the Herbarium of the University of California at Berkeley.

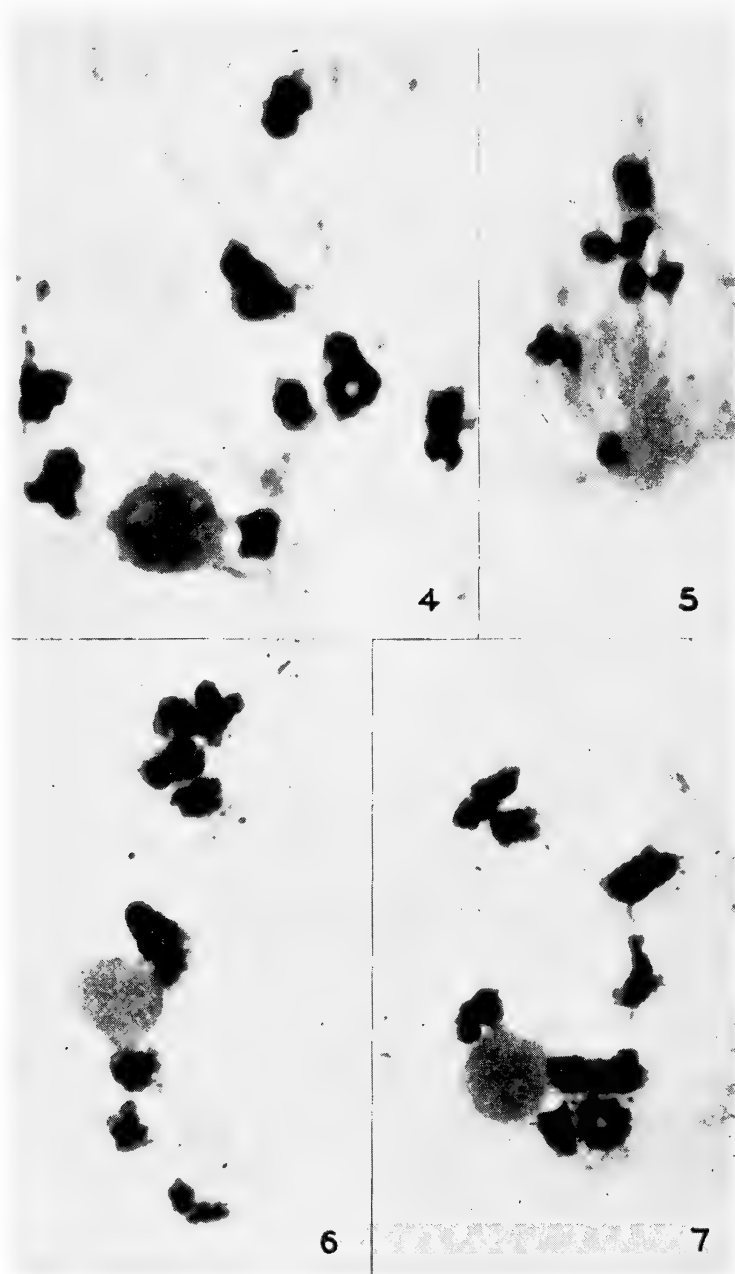
* All localities are in California unless otherwise noted.

closely related genus of *Ranunculus*, which like *Myosurus* has large-Ranunculus-type chromosomes (Langlet, 1932), ranges from $n=7$, $n=8$ to $n=64$ (Darlington and Ammal, 1955).

When the problem of the existence of sympatric biotypes was first suggested (Stone, 1959), it was hoped that cytology might provide some



FIGS. 1-3. Somatic metaphase chromosomes and idiograms of three *Myosurus* species: 1, *M. sessilis*, shoot-apex squash, $\times 2000$; 2, *M. minimus* var. *filiformis*, root-tip squash, $\times 2200$; 3, *M. cupulatus*, root-tip squash, $\times 1360$.



FIGS. 4-7. Meiotic configurations of *M. sessilis* and subspecies: 4, *M. sessilis*, diakinesis, $\times 1850$; 5, *M. sessilis*, metaphase I, $\times 1850$; 6 and 7, *M. sessilis* subsp. *alopecuroides*, diakinesis, $\times 1850$.

clue to the mechanisms involved in isolation. This hope, unfortunately, was not realized. A survey of chromosome numbers in nine heterogeneous California valley populations (Mason, 1957; Stone, 1957), representatives of two high-mountain species, and a collection from Norway, however, showed only diploid plants with $n = 8$ and $2n = 16$. Although no deviations from the basic number of 8 were found, it is possible that specialized biotypes found in disjunct pools throughout California might prove to be exceptions. Additional information was sought in a karyotype study of three of the most extreme morphological types (figs. 1, 2 and 3). Here again, no differences could be established.

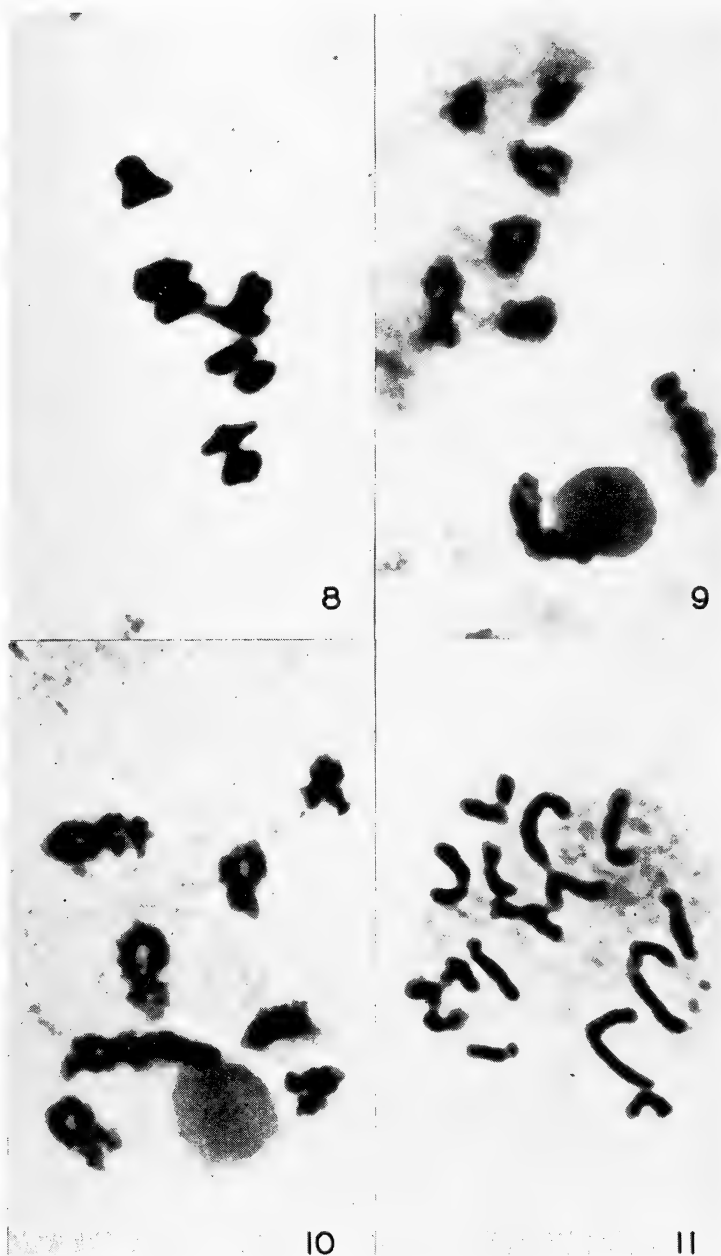
MATERIAL AND METHODS

All of the material examined cytologically was grown in the Botany Department greenhouse, University of California, Berkeley.

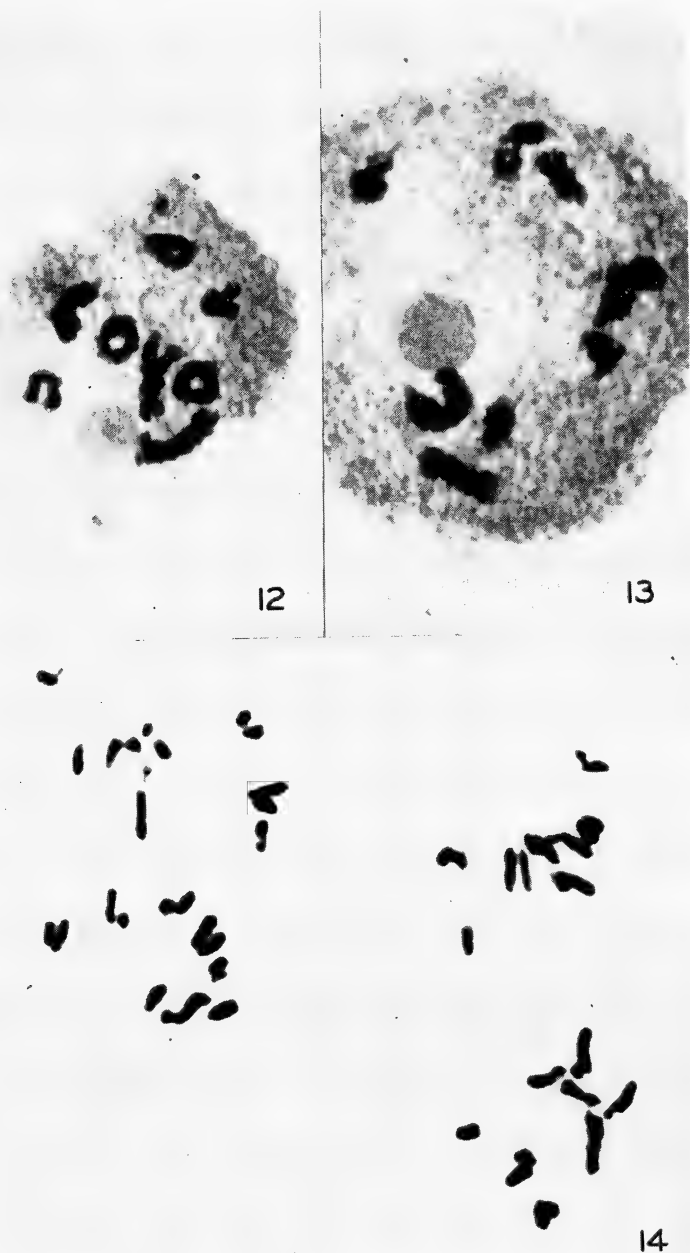
Mitotic stages were most readily obtained from the root tips of young seedlings or from the embryonic tissues of leaf bases and shoot apices. Fixation with acetic-alcohol (1:3) and staining with iron aceto-carminé proved satisfactory in root-tip squashes of young seedlings. Root tips of more mature individuals, however, were extremely difficult to squash, hence special techniques were found necessary. The following four-step process worked well on material examined immediately after squashing: (1) fixation of root tips in acetic-alcohol for 24 hours; (2) pre-staining of the material in aceto-carminé at 60° C. for 2 hours; (3) hydrolyzing in 1N HCl at 60° C. for 1 hour; and (4) washing in distilled water for 15 minutes, after which the material was stored in 70 per cent ethanol. Processed root tips were then squashed using additional iron aceto-carminé stain. Cells hydrolyzed in such a manner have light-stained nucleoli and dark stained chromosomes, and thus are quite favorable for observation of chromosome-nucleolar associations in mitotic prophase. Apparently there is a differential reduction of acidity in the pre-stained nucleus during the hydrolysis (Rattenbury, 1952). Due to the obvious difficulty of chromosome distortion in squashes, paraffin-section methods were tried. However, the minute size of the secondary roots (0.1–0.2 mm. in diameter) and the restricted meristematic region made sectioning efforts fruitless.

Stages of microsporogenesis were used in the study of the meiotic chromosome behavior. When obtained, active pollen mother cells were extremely useful in determining chromosome number, size, and pairing relationships. Three features affecting satisfactory results should be noted: (1) the period of active microsporogenesis; (2) the position of the bud; and (3) the size of the bud and stamens.

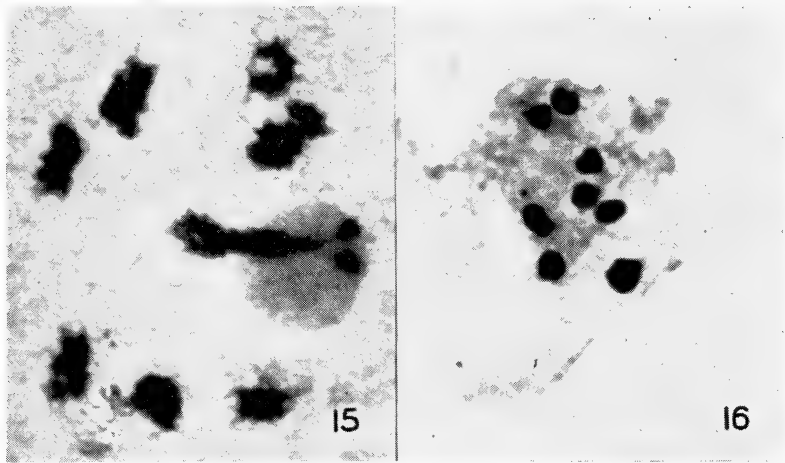
The period of microsporogenesis was found to be of extremely short duration. Out of a total of four or five young buds on a plant it was common to find that most had already matured, while the remainder were premeiotic. Possibly, poor greenhouse conditions were responsible for the shortened meiotic period, but judging from the luxuriant specimens, this



FIGS. 8-11. Meiotic and mitotic configurations of *M. minimus* and subspecies: 8, *M. minimus* subsp. *apus*, metaphase I, $\times 1850$; 9, *M. minimus* subsp. *apus*, diakinesis, $\times 1850$; 10, *M. minimus*, diakinesis, $\times 1850$; 11, *M. minimus*, mitotic metaphase, $\times 2800$.



FIGS. 12-14. Meiosis in *M. minimus* var. *filiformis*: 12-13, diakinesis, $\times 1850$; 14, anaphase II, $\times 1500$.



FIGS. 15–16. Meiosis in two montane species of *Myosurus*: 15, *M. aristatus* subsp. *montanus*, diakinesis showing attachment of chromosome No. 1 (large satellited one) with nucleolus, $\times 2000$; 16, *M. cupulatus*, metaphase I, $\times 2000$.

does not seem likely to be the case. Perhaps a condition such as this, where meiosis occurs at a very early stage and over a short period of time, has a selective advantage in plants that survive in ephemeral environments such as vernal pools.

In all biotypes of *Myosurus* examined, meiosis occurs before peduncle elongation takes place. The meiotic buds are found buried deep in the basal rosette of leaves and peduncles of the more mature flowers. Meiotic buds are usually less than 1.5 mm. in length and hence are extremely difficult to find and remove. Killing and fixing of the entire plant, however, was found practical. Buds were removed under a dissecting microscope at $30\times$, and flower dissection was completed at $60\times$, with one stamen (anthers 0.3–0.5 mm. long) at a time being removed for squashing. Plants used for meiotic studies were fixed either in acetic-alcohol or in Linnert's fixative.

The photomicrographs in the accompanying figures were made using a Bausch and Lomb compound microscope having either a $90\times$ (N.A. 1.30) or a $60\times$ (N.A. 1.40) apochromatic objective and a $15\times$ compensating eyepiece. The magnification of each figure is noted in the legend of the figure.

RESULTS

Mitotic Chromosome Number and Morphology

Detailed cytological studies were limited to the Manning Flat, Maxwell, and Willows populations (Table 1), but a survey of additional biotypes from the other California Valley populations established a single chromosome number of $2n = 16$. The photographs of figures 1–3, and 11, are representative of the mitotic squashes that were observed in this study. The

generic karyotype consists of 5 submedian and 3 subterminal chromosomes. The largest of the set bears a conspicuous satellite. The idiograms are based on the average of the homologous pairs of chromosomes, as measured in the corresponding photographs. The arbitrary classification of the centromere is based on the relative length of the two arms (Goodspeed, 1945); median (m), arm ratio 1:1; submedian (sm), arm ratio greater than 1:1 but less than 3:1; subterminal (st), arm ratio 3:1 or greater. It is quite apparent that although the satellited chromosome fits in the submedian class, it is very close to the median class, and for all practical purposes it can be considered as such. The conspicuous uniformity in the size gradient from the large satellited chromosome to the smallest subterminal chromosome is common to all three taxa. The most notable difference between the idiograms is the absolute size of the chromosomes. For example, the satellited chromosome is about 6 microns in figure 1, 6 microns in figure 2, and 7 microns in figure 3. As cell size and chromosome size are more or less interdependent and seem to fluctuate considerably in the same plant, no significance was attached to the slight differences in length.

Examination of Norwegian material (fig. 11) has proven the chromosome number to be identical to that of California specimens. Ehrenberg's polyploid counts still remain to be verified.

Meiotic Chromosome Number and Pairing Relationships

Diakinesis (figs. 4, 6, 7, 9, 10, 12, 13, and 15) was by far the most common meiotic stage encountered. In part, this occurrence might be attributed to the selected time of fixation: it was found that best results were obtained if fixation was limited to the time between 12 noon and 2 p.m. Infrequently, metaphase I stages (figs. 5, 8, and 16) were found. Later stages in the meiotic sequence were so rare that only two pollen mother cells were observed in the anaphase II stage (fig. 14). The second meiotic anaphase is frequently useful in denoting karyotype differences (Chambers, 1955) and in the case of figure 14 it is possible to verify centromere positions established in mitotic preparations. All of the figures show 8 pairs of chromosomes with no indication of pairing difficulties. It is of interest to note the association of the large satellited chromosome (No. 1) with the nucleolus in the diakinesis figures.

SUMMARY

Mitotic and meiotic chromosome counts have been made for each of seven taxa of *Myosurus*, on six of which no counts have previously been reported. All examined specimens of the genus *Myosurus* displayed a diploid number of 16, and a haploid number of 8 chromosomes, with no meiotic irregularities.

Tulane University,
New Orleans, La.

LITERATURE CITED

- CHAMBERS, K. 1955. A biosystematic study of the annual species of *Microseris*. Contr. Dudley Herb. 4:207-312.

- DARLINGTON, C. D., and E. K. JANAKI AMMAL. 1945. Chromosome atlas of cultivated plants. Allen and Unwin, London. 397 pp.
- DARLINGTON, C. D., and A. P. WYLIE. 1955. Chromosome atlas of flowering plants. Allen and Unwin, London. 519 pp.
- EHRENBERG, L. 1945. Kromosomtalen hos några kärlväxter. Bot. Not. 4:430-437.
- GOODSPEED, T. H. 1945. Chromosome number and morphology in *Nicotiana*. VII. Karyotypes of fifty-five species in relation to a taxonomic revision of the genus. Univ. Calif. Publ. Bot. 18:345-367.
- GREGORY, W. C. 1941. Phylogenetic and cytological studies in the Ranunculaceae. Amer. Phil. Soc. Trans., New Series, 31:443-521.
- HOCQUETTE, M. 1922. Observations sur le nombre des chromosomes chez quelques Renonculacées. C. R. Soc. Biol. Paris, 87:1301-1303.
- LANGLET, O. 1932. Über Chromosomenverhältnisse und Systematik der Ranunculaceae. Svensk. Bot. Tidskr. 26:381-400.
- MANN, G. 1892. The embryo sac of *Myosurus minimus* L. Trans. and Proc. Bot. Soc. Edinburgh, 19:351-428.
- MASON, H. L. 1957. Flora of the marshes of California. Univ. of Calif. Press, Berkeley. 878 pp.
- RATTENBURY, J. A. 1952. Specific staining of nucleolar substance with aceto-carmine. Stain Tech. 27:113-120.
- STONE, D.E. 1957. Studies in population differentiation and variation in *Myosurus* of the Ranunculaceae. Ph.D. Thesis. Univ. of Calif., Berkeley.
- . 1959. A unique balanced breeding system in the vernal pool mouse-tails. Evolution 13:151-174.

VARIATION IN SECTION TRIGONOPHYLLAE OF NICOTIANA

PHILIP V. WELLS

Section *Trigonophyllae* of the genus *Nicotiana* is peculiar to the warm deserts of southwestern North America, and ranges from California to Texas and southward locally as far as Oaxaca. The section, as defined by Goodspeed (1954), includes two species: *N. trigonophylla* Dunal, the range of which coincides with that of the section, and *N. Palmeri* Gray, which is apparently found only in southwestern Utah and western Arizona.

During the course of an ecological investigation of *N. trigonophylla* throughout its range in the United States, the writer encountered facts which cast doubt on the validity of the specific rank of the taxon *N. Palmeri*.

The two members of the section *Trigonophyllae* are segregated as follows by Goodspeed (1954) in his key and text:

- Calyx 8-11 mm. long; corolla 12-23 mm. long, limb 3-4 mm. wide, erect in bud; seed ca. 0.5 mm. long; cauline leaves obtuse to acuminate....*N. trigonophylla*
 Calyx 15-17 mm. long; corolla 23-32 mm. long, limb 5-6 mm. wide, oblique in bud; seed ca. 0.7 mm. long; cauline leaves acute to acuminate.....*N. Palmeri*

Both taxa have the same chromosome number (12 pairs) and Kostoff (1943) reported that F₁ hybrids between the two show twelve homologous pairs of chromosomes at meiosis.

The writer visited several of the major herbaria¹ of the United States and examined the collections of *Nicotiana*, section *Trigonophyllae*. Only

nine collection numbers were encountered which were labelled or annotated as *N. Palmeri*. Of these, one was an intermediate mentioned by Goodspeed (1954), and of the remaining eight specimens only two possessed corollas appreciable larger than those of *N. trigonophylla*: 1) *Keck 4255* (UC) Gillespie Dam, Maricopa County, Arizona, March 22, 1936. "In lava rock at cliff base." 2) *Gould 1611* (NY) St. George, Washington County, Utah, April 20, 1942. "Southern slope of Black Hill . . . on rock ledges and among volcanic boulders." Both of these specimens have corollas more than 30 mm. in length. This is larger than the type collection (*Palmer 433*), which is intermediate between these extremes and *N. trigonophylla*.

In the herbarium at Dixie College at St. George, Utah, there were seven collections of section *Trigonophyllae* from the basalt-capped mesa just west of St. George (the site of *Gould 1611*). Of these, only one was labelled *N. Palmeri*; the other six (including one determined by I. Tidestrom) were labelled *N. trigonophylla*. None were more than intermediate between the two taxa. On the other hand, the writer has grown plants from seed collected from this same site which produced corollas 27 mm. in length, which is within the size range for the flowers of *N. Palmeri*.

Specimens and seed were collected over a large part of the range of section *Trigonophyllae* in the United States. Measurements of various taxonomic characters were made both on collected plants and on plants grown from seed in the greenhouse. The results are presented in Table 1, where a number of size classes are established for each character investigated. The number of measurements falling within each size class is given, thus illustrating the modal class and the range of variation. For the greenhouse-grown plants each figure represents the number of plants having that particular mean character size, while for the collected specimens, each figure indicates the number of measurements falling in a size class.

The populations investigated show a trend toward *N. Palmeri* characters as one approaches the Washington County, Utah area. Whether one regards *N. Palmeri* as a distinct species or prefers to sink it to the subspecific or varietal level, it is apparent that the two taxa are not clearly delineated, but intergrade with respect to all characters measured. This morphological intergradation is probably best interpreted in a topoclinal sense, since no ecological gradients appear to be involved. In the range of *N. Palmeri*, section *Trigonophyllae* occupies its three usual ecological niches: 1) bedrock outcrops and talus; 2) dry washes; 3) ruderal sites (roadsides, etc.), but it is most prevalent in the first mentioned (Wells, 1959).

¹ The following institutions were visited: Bureau of Plant Industry (Beltsville, Md., Missouri Botanical Garden, St. Louis, New York Botanical Garden, Rancho Santa Ana Botanical Garden, Claremont, California, University of California, Berkeley, and the United States National Herbarium, Washington, D.C.

The tendency of plants of section *Trigonophyllae* to occur in small, isolated populations, and the localization of plants showing *N. Palmeri* characters in certain northwestern portions of the range of the section, suggest the operation of the Sewall Wright effect in bringing about differentiation. A related possibility is the selection of larger flowers by some local pollinator in the *N. Palmeri* range.

The taxon *N. trigonophylla* Dun. is acknowledged by Goodspeed (1954) to be a variable one. With respect to the validity of *N. Palmeri*, Goodspeed (1945) wrote: "... *N. Palmeri* is morphologically so closely related to *N. trigonophylla* as doubtfully to deserve specific recognition ...". In his 1954 monograph, he wrote: "This species (*N. Palmeri*) is obviously close to *N. trigonophylla*. It is distinguishable even from large flowered races of the latter by the greater coarseness throughout, by longer corolla, and by broader, whiter, more horizontal limb with lobes at times slightly concave. *Maguire and Blood 1456*, 15 miles SW of Leeds (Washington Co.), Utah (UC) is an example of an intermediate between the two."

In the herbarium of the New York Botanical Garden, there is a series of collections of section *Trigonophyllae* from Sonora and Baja California. On one of the herbarium sheets (*MacDougal 41*), there are some remarks by a reviewer of these collections (unsigned). In summary, he finds the material "not uniform but contains 2 forms with very different pubescence. One is densely glandular villous-tomentose and is so oily as to heavily stain collecting paper. The two forms deserve nomenclatural recognition, but at present it seems impossible to determine which is typical form. *N. Palmeri* Gray of Arizona seems intermediate in its characters, but nearest to eglandulose form." The writer also found wide variation in several characters (including flower size) in the Mexican collections of section *Trigonophyllae*. It seems likely that an intensive study of the *N. trigonophylla* complex in Mexico might uncover variants at least as divergent as the currently accepted *N. Palmeri*.

Considering the variability of *N. trigonophylla* and the continuous intergradation between it and *N. Palmeri*, and also the very meager representation of the latter taxon in herbaria, it does not seem too conservative to relegate *N. Palmeri* to subspecific or varietal status. This, in fact, has already been done by Marcus E. Jones (1908) who reduced *N. Palmeri* Gray to *N. trigonophylla* Dun. var. *Palmeri* (Gray) Jones.

Department of Biological Sciences,
California State Polytechnic College,
San Luis Obispo, California.

LITERATURE CITED

- GOODSPEED, T. H. 1945. Cytotaxonomy of *Nicotiana*. Bot. Rev. 11:533.
———. 1954. The genus *Nicotiana*. Chronica Botanica, Waltham, Mass.
JONES, M. E. 1908. Contr. West. Bot. 12:52.
KOSTOFF, D. 1943. Cytogenetics of the genus *Nicotiana*. State Printing House, Sophia.
WELLS, P. V. 1959. An ecological investigation of two desert tobaccos. Ecology 40: 626-644.

STUDIES ON SECOTIACEOUS FUNGI VII.
SECOTIUM AND NEOSECOTIUM.ROLF SINGER AND ALEXANDER H. SMITH¹

We have had occasion to mention the genus *Secotium* in the narrower sense as based on *Secotium gueinzii* Kunze from South Africa. These references to *S. gueinzii* in the preceding parts of our studies on secotiaceous fungi were motivated by the necessity of comparing the characters of the type species of the genus with the characters of the other genera of the family as proposed in our previous papers.

We have now arrived at the question: what is the position of *Secotium gueinzii*, and which other species of *Secotium* are close to it?

In the first place we wish to redescribe the species to facilitate the comparison.

SECOTIUM Kunze, Flora 23:321. 1840.

SECOTIUM GUEINZII Kunze, l.c. p. 322.

Gastrocarp convex, truncate below or not, always deeply sinuate underneath along the apex of the stipe (like *Endoptychum depressum*), semiglobose to campanulate, 30–60 mm. broad, about 32–42 mm. tall.

Peridium (inner) tessellate (with canal-like depressions), not gelatinized, white-buff (dried fuscidulous-yellowish), sometimes covering the gleba completely, sometimes pulled back (down) to expose some part of gleba; gleba loculate, with small chambers which do not show lamellar arrangement in any form but are winding, irregular, and unequal, not pulverulent, the walls white, thin, ochraceous buff to light brownish and said to have been pale olive, the exposed surface of gleba (if any) vertically surrounding the apex of the stipe.

Stipe up to 70 mm. long and 5–10 mm. broad at apex, up to 22 mm. broad at base, buffish colored, apparently smooth and glabrous, dry, stuffed; columella continuous with the stipe and either percurrent or not, if not, then sending out tramal plates with thick branches which merge with the normal thin tramal plates making up the loculi, at times changing direction in relation to the stipe and becoming oblique rather than vertical, broadened into the upper portion of the peridium if percurrent, white; volva said to be present, whitish, eventually disappearing except at the base of the stipe where it appears cothurnate, a distinct annular veil such as seen in *Endoptychum depressum* not described, not seen in the fragments available, and not clearly shown in illustrations. Context white, dry-fleshy, probably when fresh somewhat like *Endoptychum agaricoides*.

Spores (8.5–) 11–14 \times (6.3–) 8.2–9.7 μ , short ellipsoid but ovate in frontal view, somewhat inequilateral in profile (asymmetric), with oblique eccentric sterigmal appendage, pale olive-melleous to melleous-

¹ Papers from the University of Michigan Herbarium and the Department of Botany, No. 1087, University of Michigan, Ann Arbor, Michigan.

hyaline, the wall thick and complex (at least four wall-layers discernible), smooth, some with an apical germ pore, or some with an apical truncation but without a demonstrable discontinuity in the wall (or else pore incomplete and spore not truncate), slightly metachromatic in cresyl blue but absorption of the cresyl blue very variable, if weakly stained, a lilac line along the endosporium visible and inner two layers sometimes remaining incolorous, when strongly stained the whole wall and interior deep blue as in spores of *Chlorophyllum molybdites*, correspondingly, with Melzer's reagent distinctly pseudoamyloid but some remaining inamyloid and a few discoloring only partly; not forming a pulverulent mass in the gleba.

Basidia about $28 \times 9.7\mu$, 4-spored, sterigmata variable, some thin and straight but oblique, some thin and slightly curved (somewhat intermediate between "agaricoid" and "gastroid"); cystidia not seen, but yellow "Pollinarien" described and illustrated by Corda.

Trama hyphous throughout, in places very slightly gelatinized, hyaline, in peridium extremely irregular but more radially arranged in outermost layer of endoperidium, the hyphae of all layers 2–6 μ in diam., inamyloid and with clamp connections.

Terrestrial on the sand steppes of the Cape of Good Hope, South Africa, Uitenhage, fruiting in summer (December). Leg. *Queinzius*, comm. M. C. Cooke (NY, part of type).

Another part of the type is at Kew (Singer has seen but not studied it, but he is certain that it is part of the same collection, which is corroborated by the fact that what little Heim communicates about the "Berkeley-type" coincides well with our findings). It is possible that part of this was also in Corda's Herbarium which is in Prague.

This species has the same essential spore-wall characters as *Endoptychum agaricoides* and *E. arizonicum*, namely the pseudoamyloid reaction, the thick, many-layered wall, and the relatively light color (varying to hyaline). In spite of these similarities, there are important differences such as the presence of a volva, non-pulverulent gleba, abundant clamp connections, and large ellipsoid spores with a germ pore. In view of these differences it appears illogical to us to place *S. queinzi* in the same genus with *Endoptychum*. This was apparently also Zeller's point of view.

However, two other species, intermediate in their characters, need to be considered here. One is *Secotium macrosporum* Lloyd. It is intermediate in such basic characters as the pulverulent gleba and degree to which clamps are present, but is strikingly distinct because of the complex ornamentation of the spores. With some modifications the spore ornamentation is the type that is found in some tropical *Lepiotas* (*Leucoagaricus*) and/or (this is significant), in the *Lycoperdaceae*. We shall discuss the affinities of this interesting species later, but considering its differences from both *Endoptychum* and *Secotium*, we cannot convince ourselves that according to any generic concept short of re-establishing *Secotium sensu lato*, can *S. macrosporum* be considered congeneric with either *Secotium* or *Endoptychum*.

This establishes *Secotium* as a monotypic genus, and necessitates establishing a new genus for *S. macrosporum*. We propose for it the new generic name *Neosecotium*, this being a New World *Secotium* and a species only now critically analyzed (Neo—new; secotium—a loculate system).

Neosecotium gen nov.

Carpophoris haud volvatis, pallidis, stipitatis, columella percurrente; gleba demum paulum vel manifeste pulveracea; sporis hyalinis leviter ochrascentibus, pseudoamyloideis, poro germinativo instructis, globosis, membrana admodum crassa reticulatim fracta ornamentatis; fibulis praesentibus sed sparsis.

Typus generis: *Secotium macrosporum* Lloyd.

Neosecotium macrosporum (Lloyd) Sing. & Smith, comb. nov.
Secotium macrosporum Lloyd, Mycol. Writ. 1:139. 1903.

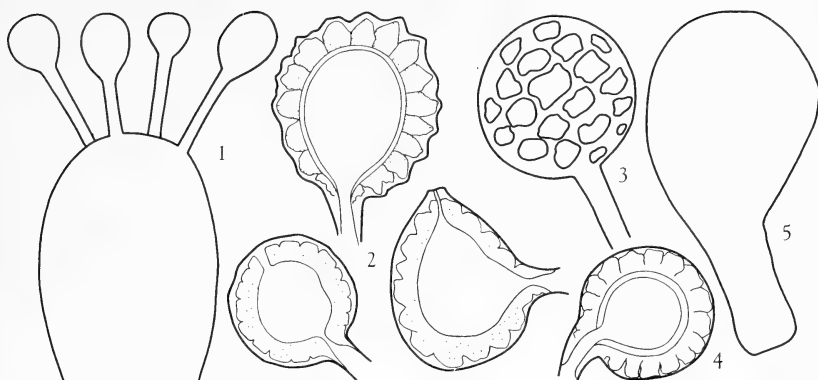
Gastrocary 1–3 cm. high and 1–2 cm. thick, subelliptic to nearly globose, the margin not separating from the stipe-columella.

Peridium smooth, avellaneous or paler, the lower portion whitish-pallid at times.

Gleba chambered at first, but somewhat pulverulent and at maturity little if any structure visible, in immature stages showing chambers oriented in an obscure lamellar orientation, about wood brown (R) near maturity or finally becoming more cinnamon, not separated from columella.

Stipe-columella percurrent, pallid throughout as dried, 2–3.5 mm. diam. in widest place (as dried), very little (2–3 mm.) projecting below the gastrocarp as a stipe.

Spores globose and 13.5–18 μ or 14–18 \times 12–15 μ and subglobose to slightly ovate, ochraceous to tawny in KOH (depending on degree of maturity), dark red-brown in Melzer's solution (pseudoamyloid), with a short to rather long sterigmal appendage as in many Lycoperdaceae, the pedicel hyaline and thin-walled except for the area where the thickening of the spore wall projects down into it slightly, centrally attached or rarely slightly eccentric; spore wall complex, at maturity with a thin hyaline perisporium which adapts itself to the configuration of the wall beneath (exosporium and possibly endosporium combined); exosporium and endosporium together 3–5 μ thick, rusty brown in KOH at maturity but nearly hyaline earlier, deep red-brown in Melzer's solution, smooth at first but soon becoming cracked into an areolate pattern and the fissures gradually deepening to produce a warty to almost echinulate effect and at this time the spore surface appearing distinctly roughened, but perisporial membrane still visible over warts and depressed into the crevices, in young stages where the inner thick wall is still hyaline an apical germ pore can be observed in some spores, and in abnormal spores a lateral beak furnished with a distinct pore is clearly evident, the pore obscured in old spores by the cracking up of the thick inner layer of the wall.



FIGS. 1-5. *Neosecotium macrosporum*: 1, upper part of basidium showing tubular sterigmata and young spores, $\times 450$; 2, mature spores in optical section, $\times 1000$; 3, surface view of nearly mature spores, $\times 1000$; 4, optical section of immature spores, $\times 1000$; 5, young basidium, $\times 450$.

Basidia large, $25-37 \times 14-17.5 \mu$, clavate to subelliptic-pedicellate, thin-walled and hyaline or the wall slightly thickened and brownish—hence the cell more persistent than usual; sterigmata typically 4 and tubular, not often tapering appreciably and the young spore acropetally attached or very rarely appearing slightly eccentric. Cystidia, none observed.

Subhymenium of broad intricately interwoven hyphae, hence in section appearing somewhat cellular from cut hyphal ends; hyphae of the peridium filamentous, many hyphal cells somewhat to markedly inflated ($4-12-18 \mu$ in diam.), the outer layer more or less radially arranged and melleous to dingy ochraceous in KOH, gradually paler toward gleba, not at all gelatinous or toward gleba only sub-gelatinous (slightly translucent in KOH); clamp connections absent to rarely present.

The type was collected near Dallas, Texas, by E. P. Ely. The best material we have seen, however, is a collection by R. Sprague, June 13, 1941, in grass plots on sandy soil at Mandan, North Dakota (NY).

This is a most interesting species in many respects: the long, tubular sterigmata which often break off leaving the upper half attached to the spore as a pedicel or appendage, the tendency of the gleba to become powdery at maturity, and the type of spore ornamentation in mature spores are all strongly reminiscent of the Lycoperdaceae, so much so, in fact, that we are inclined to believe that *N. macrosporum* actually does represent a true link connecting the Secotiaceae to that group. The outer surface of the dried peridium is almost *Calvatia*-like in texture, but this, of course, may not have any phylogenetic significance beyond that indicated by the type and arrangement of the hyphae of the outer zone of the peridium.

The pallid to avellaneous tone of the mature gastrocarp and its texture are also reminiscent of *Lepiota naucina*. Actually, aside from the shape

of the spore and the peculiar way in which the inner wall layers break up, the spores themselves show resemblances to those of *Macrolepiota* and *Leucoagaricus* by the presence of a germ pore (though it is obscured at maturity) and the strong pseudoamyloid reaction of the thick inner wall. Also the spores are metachromatic in Cresyl blue—at least the pale colored spores are. These characters appear to us to connect *Neosecotium macrosporum* to the Agaricales, family Agaricaceae sensu Singer, and very likely in the vicinity of *Chlorophyllum* and *Macrolepiota*. Hence we have here a connecting link, as we see it, between the Lycoperdaceae on the one hand and a family of agarics on the other.

As far as we are aware, this is a heretofore unsuspected connection between the two groups, and when viewed in this way it is cause for much interesting speculation on the course which evolution has followed. Since in this series of papers we are not discussing the direction of evolution, we shall limit ourselves to considerations which we believe to be based on facts as follows:

The lycoperdaceous fungi show a wide range of spore color just as does the family Agaricaceae, and, though the spores in the Lycoperdaceae are small, many show a sufficiently similar type of ornamentation to make it imperative that spore structure in that order now be studied by the techniques in use for the study of spores in the Agaricales.

The problem of the powdery gleba in the Lycoperdaceae is now no problem at all as far as its being an obstacle to ascertaining connections to the Agaricales. In a number of species of *Agaricus* the gills become very soft and almost collapse after maturity, and in carpophores which did not open but which dried out *in situ* it is a simple matter to understand how these structures could break down to a powdery consistency. The presence of a highly developed capillitium is certainly to be regarded as an advanced character in the Lycoperdaceae, but this, no matter from which source one derives the Lycoperdaceae—the agarics or lower Gastromycetes—does not offer any serious hurdle to establishing relationships in either direction. Any hymenophoral trama with thick-walled hyphae could easily give rise to “capillitium” if the remaining trama consisted of thin-walled perishable hyphae. There is no reason why thick-walled hyphae should not appear “de nova” in the glebal trama of Gastromycetes in more than one evolutionary series, since wall-thickenings of hyphae are one of the commonest types of hyphal adaptation in the fungi as a whole.

The second species of *Neosecotium* was found among the collections of *Arcangelliella* in the Zeller Herbarium. A redescription of it follows:

Neosecotium africanum (Lloyd) comb. nov. *Octaviania africana* Lloyd, Myc. Writings 7:1142. 1922. *Octaviania africana* Verwoerd, S. Afr. Journ. Sci. 22:164. 1925. *Arcangelliella africana* (Lloyd) Zeller & Dodge, Ann. Mo. Bot. 22:365. 1935.

Fructifications spherical, 10–15 mm. thick, drying cinnamon-brown to

TABLE 1. COMPARATIVE FEATURES INDICATING INTERMEDIATE POSITION OF NEOSECOTIUM MACROSPORUM BETWEEN ENDOPTYCHUM ARIZONICUM AND SECOTIUM GUEINZII.

	<i>Endoptychum arizonicum</i>	<i>Neosecotium macrosporum</i> (<i>Secotium macrosporum</i>)	<i>Secotium gueinzii</i>
SEPTA	without clamp connections	some with, some without clamps	with clamp connections
VOLVA	none	none	present
PERIDIAL SURFACE	rough but not tessellate	smooth	tessellate
GLEBA	pulverulent (strongly)	pulverulent (moderately)	non-pulverulent
SPORES			
ORNAMENT	smooth	ornamented	smooth
SIZE	small	large	large
SHAPE	subglobose	globose	ellipsoid
PORE	none	present	present

Dresden brown; peridium hard, duplex, the outer layer 140–160 μ thick, composed of closely woven slender, hyaline hyphae 1.5–2 μ in diam., the inner layer 375–400 μ thick, composed of hyaline, more loosely woven septate hyphae 3–4 μ in diam., “with lactiferous ducts” . . . Zeller & Dodge, separable; gleba drying from ferruginous to snuff brown; tramal plates 15–30 μ thick; basidia clavate, 23–30 \times 7–8 μ , sterigmata 10–15 μ long and filiform.

Spores (giant spores) 17–20 \times 14–16 μ , “normal” spores 13–15 \times 10–13 μ , subglobose to broadly ellipsoid; sterigmal appendage pedicellate; dingy yellowish in KOH, *dark red-brown* in Melzer’s reagent (pseudoamyloid); ornamented and thick-walled, inner wall about 2 μ thick, outer wall broken up into a pattern of broad obtuse to flattened warts due to the cracking of the wall; no germ pore found.

The description of the spores was taken from the part of the type in the Zeller Collections of the New York Botanical Garden. The hymenium and tissues of the fruiting body failed to revive sufficiently for critical study. It is more than evident to us that because of the pseudoamyloid spores with their characteristic ornamentation the species belongs in *Neosecotium* even though in the material available we failed to establish the presence of a germ pore. The hard, brown peridium should amply distinguish *N. africanum* from *N. macrosporum*. From what we were able to ascertain from the limited material available, it appears to us that *N. africanum* is more gastroid than *N. macrosporum*, in fact may represent a distinct genus at the level of *Martellia*. Because it represents a different level of evolution, it is not included in the chart with the other distinctly secotiaceous species.

Naturally, the genera *Endoptychum*, *Neosecotium*, and *Secotium* form a definitely circumscribed and sharply outlined group—a tribus or sub-

family—which may also contain such genera as *Polyplocium* Berk., *Gyrophrangium* Mont., and *Longula* Zeller.

Since we do not wish to enter such intricate questions of purely gastro-mycete taxonomy as the possibility of maintaining all three last-named genera (which seem to us extremely close to each other), and since our experience with them is relatively limited, we prefer to omit these genera for the time being. However, their close relationship to *Secotium sensu stricto* as well as *Endoptychum* cannot be overlooked.

REVIEW

Comparative Morphology of Vascular Plants. By ADRIANCE S. FOSTER, and ERNEST M. GIFFORD, JR. 555 pp., 213 figs. W. H. Freeman, San Francisco. 1959. \$9.00.

The literature of vascular plant morphology has been greatly enriched by this new textbook by two prominent teachers and researchers at the University of California at Berkeley and Davis. In contrast with other morphology texts that have appeared in recent years, this is a product of men who have devoted their entire careers to the higher plants. As a result, the book is organized in a manner that emphasizes morphological problems of current interest in this area, with subdued treatment of the burning questions of morphology of the early years of this century that are currently only of historical interest. This book is likely to enjoy a long active life as a textbook and reference work, therefore a detailed review seems justified.

A unique feature that sets apart "Comparative Morphology" from earlier textbooks is the organization of material into two sections. In the first part, consisting of six chapters, the principal characteristics of the vascular plants are surveyed in a comparative fashion; in the second part individual chapters are devoted to treatments of the plant groups in systematic sequence. The classification system of Tippo is followed throughout. Extinct groups are treated in an integrated manner alongside their living relatives, but the emphasis is on modern plant types. Detailed descriptive material is not presented for its own sake, but rather as evidence for morphological or phylogenetic conclusions. The detail might be described as interpretative and illustrative rather than as encyclopedic.

The opening chapter tells the beginning student what morphology is all about. There is a discussion of the concept of homology, and of the kinds of morphological evidence that have proved most useful in reconstructing concepts of phylogeny, such as ontogeny, adult form, and the fossil record. The frontiers of modern experimental morphology and morphogenesis are described briefly and some pertinent unanswered questions are posed. The following chapter deals with the overall characteristics of the phylum of vascular plants, giving an outline of a typical life cycle involving an alternation of generations. The existence of apospory and apogamy and the significance of these phenomena on the classical theories regarding the origin of alternate generations is discussed. The phylum is then divided into the usual four subphyla of Eames and Tippo.

Four chapters dealing with the principal areas of morphological investigation are devoted to the vegetative sporophyte, the sporangia, the gametangia, and to embryogeny. Under the heading of vegetative sporophyte are included discussions of the general structure of shoot and root, types of branching, types of leaves, microphylls versus megaphylls, and the phylogenetic origin of leaves according to Bower. The Telome Theory is presented briefly. The area of plant anatomy is entered with a discussion of the problems of classification of tissues and tissue systems. The system of Sachs is presented, and the structure and development of the principal tissues are

described. The chapter closes with a résumé of the historically important Stelar Theory. In this section the uses of the terms dictyostele and eustele are clarified.

The chapter on sporangia describes their function, position, and the organization of sporophylls into strobili in some groups. The structure and development of the two types of sporangia, the eusporangium and the leptosporangium are described, with an excellent series of comparative developmental drawings. The phylogenetic significance of the presence of two sporangium types is discussed. The following chapter on gametangia contrasts antheridia with archegonia in development, structure, and position. The concluding chapter in the first section of the book deals with embryogeny; the parts of embryos, polarity, and the development of the embryo from the zygote. The phylogenetic aspects of the study of embryo development are discussed.

The second section of the book opens with three chapters dealing with the subphyla usually known as the lower vascular plants. The Psilopsida are introduced with an historical treatment of their discovery, followed by synopsis of their classification into two orders and three families. *Rhynia*, *Horneophyton*, and *Asteroxylon* are described. Treatment of these fossils is limited to their general organography and anatomy. *Psilotum* and *Tmesipteris* are covered in much greater detail. Included in the description of the sporophyte structure is a discussion of the interpretation of the nature of the stem appendages, and of the multilocular sporangia found in these genera. The gametophyte generation is discussed in greater detail than is usual in recent texts, incorporating the results of contemporary workers like Bierhorst. The brief section on embryo development is followed by a concluding summary for the group. In the presentation of the details of structure and development of the sporangia, gametangia, and embryo, the earlier introductory chapters on these organs serve as a basis for comparison. In the usual treatment which lacks such introductory chapters, the organs of *Psilotum* must be studied by the beginning student, detached from the reality of the plant world that he knows.

The Lycopsida are treated in similar fashion, but here the living genera *Lycopodium* and *Phylloglossum* are described first, followed by the extinct *Protolépídodendron* and *Baragwanathia*. Then follow *Selaginella*, the Lepidodendrales, *Isoetes*, and the Pleuromeiales. Throughout this chapter much recent research is presented, along with the necessary details of structure and development that are part of the usual subject matter. The chapter on the Sphenopsida follows, using the same pattern of presentation. *Equisetum* is described first in detail, followed by a brief statement on *Hyenia*, *Sphenophyllum* and *Calamites* conclude the subphylum.

The Pteropsida include the vast majority of living vascular plants and are described under a series of ten chapter headings. The first is a brief introductory description of the group, followed by another chapter which introduces the Filicinae. This chapter includes a very brief discussion of fossil fern foliage in general, and of the Coenopteridales in particular. The taxonomic summary for the ferns is included here, followed by a list of critical areas of morphological study compiled by Bower. The Eusporangiate Ferns and Leptosporangiate Ferns are treated next under separate headings. The latter group, which includes most living fern genera, is treated as a whole in great detail. Excellent series of drawings illustrate the degrees of compounding of fern fronds, variations in venation patterns, variation in sorus structure and position, the development of the sporangium, sporangium structure and various types of annuli, types of sorus in regard to order of maturation of the sporangia. The vast array of stele types found in the ferns is illustrated by an excellent series of photomicrographs. The gametophytes and embryos are described in the same manner as in the lower groups. A section dealing with special problems in fern morphology discusses "phyletic slide" and the relationship between sorus position and phylogeny. Recent work in experimental morphology of the ferns by Wardlaw and others is carefully reviewed. A brief résumé of the problems of fern systematics is included, illustrating the relationship between morphology and phylogeny, between phylogeny and classification. In the course of the systematic treatment, the principal families are briefly described, with fuller treatment of the Marsileaceae.

The Gymnosperms are covered by four chapters. The first is an introductory

conspectus of the group which includes brief treatments of the extinct orders Cycadofilicales, Cordaitales, and Bennettitales. The development and structure of the seed are covered here, including the details of ovule ontogeny, megasporogenesis, the formation of the megagametophyte, pollination, and fertilization. This discussion is followed by a brief statement on embryogeny and seed maturation. The second chapter in this series is devoted to the living cycads and *Ginkgo*. Megasporophyll evolution is illustrated by drawings of various cycads; the cycad life cycle by another series. The details of ovule development and of embryogeny not found in the introductory chapter are included here. The Coniferales occupy the third chapter and are introduced by a systematic treatment of the principal families. This is followed by the usual section on organography and anatomy. Florin's work on Paleozoic and Mesozoic conifers is reported in connection with leaf and strobilus evolution and structure. The life cycle of modern conifers is illustrated by *Pinus*. Included here are the details of fertilization, embryogeny and seed development. Then other conifers are compared with *Pinus*. The final chapter on the Gymnosperms deals with the Gnetales. The structure and life cycle of *Ephedra* are presented in detail, followed by a brief statement of the differences between *Ephedra* and the other genera, *Gnetum* and *Welwitschia*.

The final section of the book consists of two chapters on the Angiosperms. The first of these chapters treats the general structure and evolution of the group, while the second is devoted to the reproductive cycle. Under general structure, leaf morphology is described in detail, with series of illustrations of venation patterns. Stem and root structure are covered more briefly, but a concise statement of modern views on nodal anatomy and its phylogenetic significance is included, as is a brief statement on wood anatomy. The major part of the chapter is devoted to the problems of floral morphology, including theories of the nature of the flower, and the impact of evidence from floral vascular anatomy and from floral ontogeny on these theories. The vast body of work on primitive woody Ranales by Bailey and his associates during the past twenty years is drawn upon for evidence on phylogeny of stamens and carpels. The last chapter on angiosperm reproduction describes microsporangium development and microsporogenesis, the development of the male gametophyte, the ovule, megasporocyte, megasporogenesis, and embryo sac, with detailed discussion of the important types of the latter. The events of fertilization, endosperm development, and embryogeny follow, with a final discussion of seeds and seedlings.

In summary, Foster and Gifford's "Comparative Morphology of Vascular Plants" is an excellent work featuring clear discussions and illustrations, with an organization that should prove a boon to morphology teaching.—SANFORD S. TEPPER, University of Oregon, Eugene.

NOTES AND NEWS

From June through late December, 1959, with the aid of a National Science Foundation grant, DR. FRITZ EHRENDORFER intensified his field and laboratory studies, started several years ago, on the genus *Galium* in the western United States. He returned to Vienna to take up his new duties as Assistant Curator of the Naturhistorisches Museum.

PROFESSOR HERBERT L. MASON, who recently was the recipient of a Fulbright award, will be taking a sabbatical year from the University of California commencing February 1. He will be in residence at the University of Auckland, New Zealand, devoting his time mainly to studies of floristic relations in the Southern Hemisphere.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$6.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany
University of California, Berkeley 4, California

Bot.



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 6

APRIL, 1960

Contents

	PAGE
THE REPRODUCTIVE STRUCTURES OF <i>FRAXINUS</i> <i>VELUTINA</i> (OLEACEAE), <i>Herbert F. Copeland</i>	161
A NEW <i>SILENE</i> FROM NORTHWESTERN CALIFORNIA, <i>A. R. Kruckeberg</i>	172
FREED HOFFMAN, <i>John L. Morrison</i>	178
CLEARED <i>CARDIOPARON LATE-ALATUM</i> LESQ., CORDAITEAN SEEDS FROM MICHIGAN, <i>J. F. Davidson</i>	180
THE BASIC CHROMOSOME NUMBER OF THE GENUS <i>NEPTUNIA</i> (LEGUMINOSAE-MIMOSOIDEAE), <i>B. L. Turner and O. S. Fearing</i>	184
HYBRIDIZATION AND INSTABILITY OF <i>YUCCA</i> , <i>John Milton Webber</i>	187
REVIEW: <i>The Physiology of Forest Trees</i> , edited by Kenneth V. Thimann, et al. (N. T. Mirov)	192
NOTES AND NEWS	192

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$6.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—**ANNETTA CARTER**

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—**JOHN H. THOMAS**,

Dudley Herbarium, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: Herbert G. Baker, Department of Botany, University of California, Berkeley, California. First Vice-president: Malcolm A. Nobs, Carnegie Institution of Washington, Stanford, California. Second Vice-president: Herbert F. Copeland, Sacramento City College, Sacramento, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: John Thomas, Dudley Herbarium, Stanford University, Stanford, California.

THE REPRODUCTIVE STRUCTURES OF FRAXINUS VELUTINA (OLEACEAE)

HERBERT F. COPELAND

The observations on floral structure and embryogeny in *Fraxinus velutina* Torrey, called the Arizona ash, which are here presented, were undertaken because an abundance of material was available; and because the facts as to Oleaceae assembled in Schnarf's (1931) *Vergleichende Embryologie der Angiospermen* were fragmentary, including no reasonably complete account of any single species.

Material was collected from trees cultivated on the grounds of Sacramento City College during the years 1957 to 1959. It was treated by routine microtechnical methods: fixed in Bouin's fluid and stained with Delafield's haematoxylin, Heidenhain's haematoxylin, or safranin and light green.

In the library, consulted when a certain acquaintance with the plant had been attained, I found out that the microscopic reproductive features of the Oleaceae are no longer poorly known; also, that there has been disagreement as to the proper place of Oleaceae in the taxonomic system. These matters are discussed in later sections of this paper.

THE TREE

Fraxinus velutina occurs near springs and along streams in western Texas, New Mexico, Arizona, and southern California. Pratt (1922?) wrote of it as apparently new in cultivation and recommended it as resistant to alkali and drought. It is widely planted in northern California, where it is seen to survive with little or no irrigation, but to flourish in watered lawns.

Munz and Lauder milk (1949) refer all plants of this species which are native in California to var. *coriacea* (Watson) Rehder, and I have been uncertain of the identity of the cultivated material. Taylor (1945) found the species diploid ($2n = 46$) and the variety tetraploid ($2n = 92$). The cultivated trees are diploid ($n = 23$), and are to be referred to the species.

As a typical ash, this is a deciduous tree bearing opposite pinnate leaves and producing samaras. It belongs to the group of ashes in which the flowers are apetalous and dioecious. Flower clusters appear in the axils of the proximal fallen leaves of the previous year during the month of February. Pollination is evidently by wind. In March, the staminate flowers fall, and the leaves begin to unfold. The samaras grow to their full size by the end of May, but the seeds are not mature until autumn. The samaras are shed, along with the leaves, in autumn storms.

The flower clusters are dense glomerules. After anthesis, the axes of the pistillate clusters become elongate, and it is seen that they are freely branched in a decussate pattern. All of the flowers or fruits of a particular

cluster are at a particular time in nearly the same stage of development; most axes bear terminal flowers; hence, the clusters are to be construed as thyrses.

MALE STRUCTURES

The staminate flower (fig. 1) consists, beyond its receptacle, of a calyx which is reduced to a minute toothed cup and of two stamens having brief filaments and prominent basifixed extrorse anthers. The vascular supply of this flower (fig. 2) consists of a cylinder of tissue originating from the two sides of a bract gap, emitting a cycle of a small indefinite number of feebly developed traces to the calyx, and then splitting into two bundles which ascend the connectives of the anthers to their summits.

The anthers are of the structure usual in flowering plants. The cells of the endothecium duly develop ribbed walls, and the dehiscence of the anthers, which occurs through the usual two lengthwise clefts, is produced by their contraction. The tapetum is of the secretion type. The nuclei of the tapetal cells divide more than once, and then undergo fusions, with the result that just before the tapetum is absorbed its cells contain varying numbers of large nuclei with varying numbers of nucleoli (figs. 3, 4).

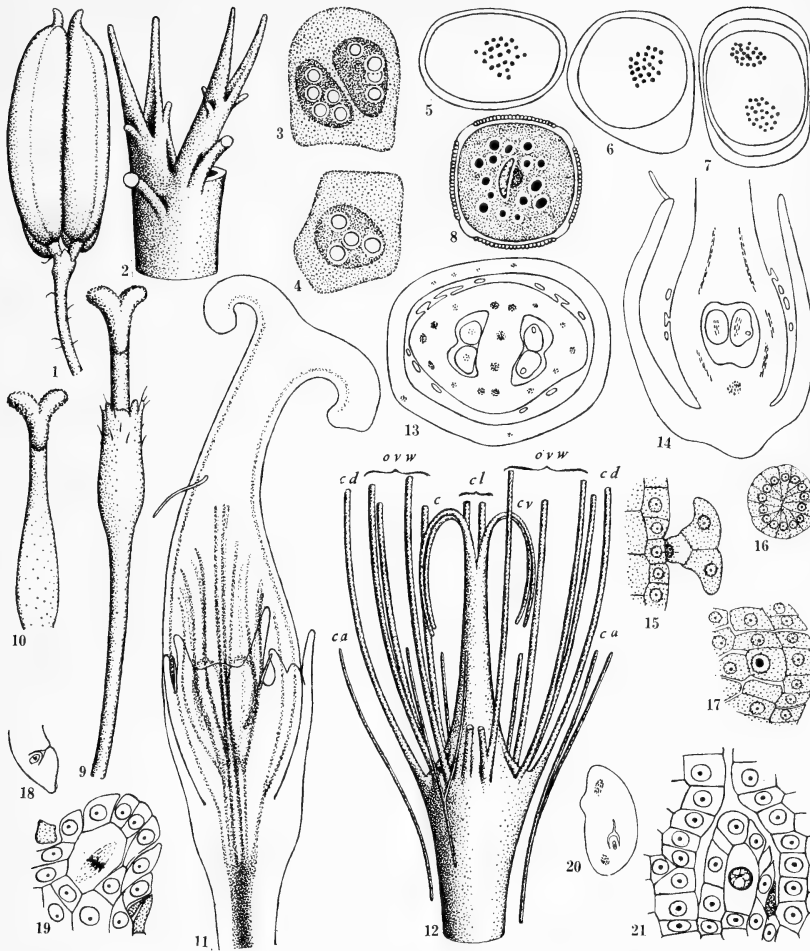
The haploid chromosome number, observed during meiosis in the pollen mother cells, is 23 (figs. 5, 6, 7). The pollen grains are separated by simultaneous furrowing. When mature, they are four-grooved, having the surfaces between the grooves finely pitted, and contain a tube nucleus and a generative cell (fig. 8).

THE PISTILLATE FLOWER

The pistillate flower (fig. 9) consists, beyond its receptacle, of a cup-shaped calyx with a dentate margin and a compound pistil of two carpels. The ovary contains two locules. The septum between the locules is punctured by a small cleft near its upper end: the upper ends of the locules are continuous. Each locule contains two ovules which are pendant from the distal area of the septum. The ovary is flattened contrary to the narrow septum (fig. 13); the flattening is moderate through most of the height of the ovary, but is greater in the upper part. The brief style is cylindrical. The stigma is of two lobes which are pressed together when the flowers are first exposed but become separate at anthesis. The stigmatic surface is papillose.

The ovary bears a moderate number of peltate trichomes (figs. 15, 16) which are of the same nature as those which occur on leaves of *Syringa* and *Ligustrum*. The pedicel and flower bear also a few simple hairs, mostly on the margin of the calyx.

The vascular system supplying this flower is as follows (figs. 11, 12). The usual cylinder of vascular tissue ascends the pedicel. The calyx contains a whorl of a varying number of feebly developed bundles which fade out below. This means that the stele in the pedicel supplies only the pistil. The stele gives rise to an outer whorl of about fourteen bundles including (a) two well-marked carpel-dorsals, respectively ascending the



FIGS. 1-21. *Fraxinus velutina*: 1, staminate flower $\times 8$; 2, vascular supply of two staminate flowers, $\times 40$; 3, 4, mature cells of the tapetum, $\times 720$; 5, 6, pollen mother cells with nucleus in heterotypic metaphase, $\times 720$; 7, pollen mother cell with nucleus in heterotypic anaphase, $\times 720$; 8, pollen grain, $\times 720$; 9, pistillate flower, $\times 8$; 10, pistil, $\times 8$; 11, pistillate flower cleared in chlorine water, $\times 20$; 12, model of vascular system in lower part of the pistillate flower, $\times 40$; 13, cross section of young ovary, $\times 40$; 14, longitudinal section of young ovary, $\times 40$; 15, 16, radial section and surface view of scale of ovary, $\times 320$; 17, archesporial cell of young ovule, $\times 320$; 18, 19, longitudinal section of developing ovule, $\times 40$, and nucellus of same showing megaspore mother nucleus in heterotypic metaphase, $\times 320$; 20, 21, longitudinal section of ovule, $\times 40$, and nucellus of same showing megaspore mother cell, $\times 320$. *ca*, sepal bundles; *cd*, carpel dorsal bundles; *cl*, carpel lateral bundles; *cv*, carpel ventral bundles; *ovw*, ovary wall bundles.

margins of the ovary and continuing up the style into the stigmatic lobes; (b) a total of about eight ovary wall bundles, being about two on each

side of each carpel dorsal; and (c) a pair of well-marked carpel-laterals at each margin of the septum. Above the level of the locules, the ovary wall bundles and carpel laterals spread apart to form two fan-like layers toward the respective surfaces of the flattened upper part of the ovary. These bundles do not enter the style, but fade out. The vascular tissue which ascends beyond the departure of the whorl just described takes the form of an attenuate cone ascending the septum of the ovary. The cone splits to form two bundles located toward the margins of the septum, and each of these, toward the summit of the septum, splits in turn into two bundles which diverge and turn down to supply two ovules lying in different locules.

OVULE AND EMBRYO SAC

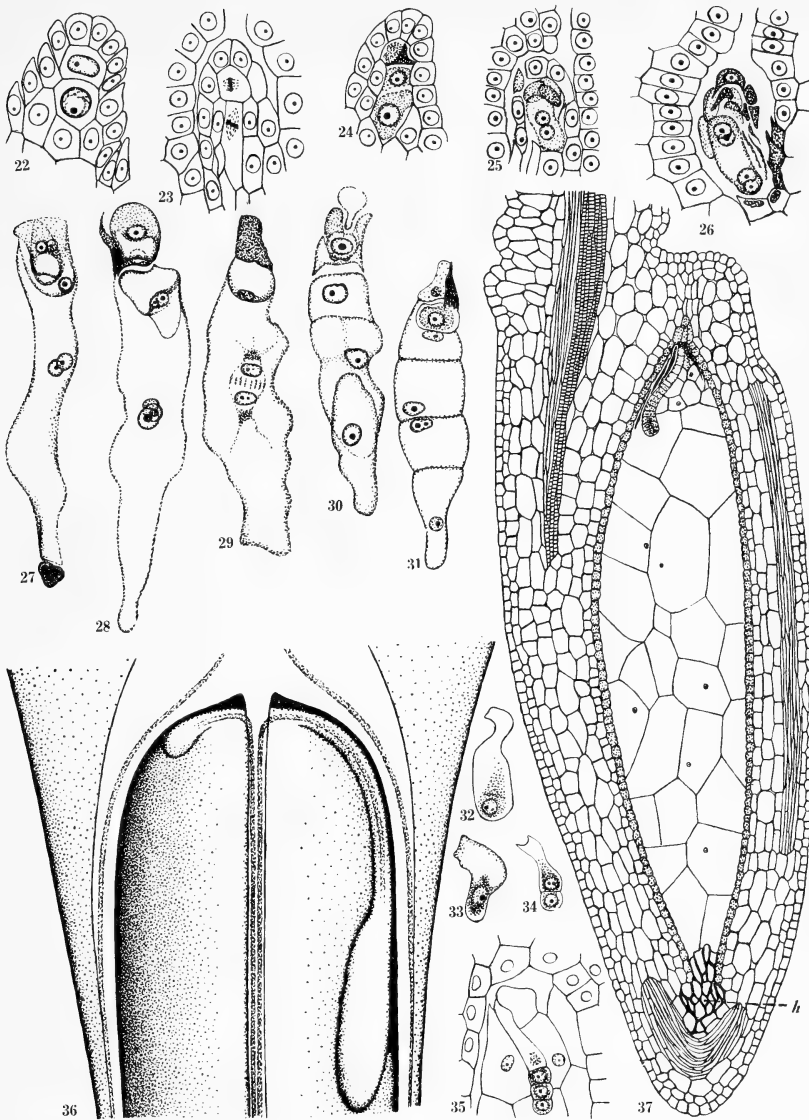
When the pistillate flowers are first exposed, before the stigmatic lobes swing apart and become receptive, one finds in each locule two immature ovules (figs. 13, 14) of the form of downward-pointing fingers. Each one contains a strand of immature vascular tissue. Each contains one hypodermal archesporial cell (fig. 17). The archesporial cells are located on the sides of the ovules which are away from the plane of the carpel-dorsal bundles: one sees them best in sections cut parallel to the septum.

The archesporial cell is itself the megaspore mother cell. It becomes elongate, and the epidermis covering it is pushed up as a scanty nucellus (figs. 19, 21). The tissue on all sides of the nucellus grows forth to form an integument. The growth is greatest on the side of the nucellus toward the original tip of the ovule, which now becomes the chalaza. The effect of this growth is to turn the nucellus toward the summit of the ovary, and to enclose it except for a narrow micropyle leading up from it (the growth of the ovule is illustrated only by two little diagrams, figs. 18, 20). The mature ovule is somewhat flattened between the septum and the ovary wall.

During the growth of the ovule as just described, spiral tracheids appear in the main bundle which runs down the raphe to the chalaza. At the same time, several additional bundles begin to undergo differentiation in the integument. These latter bundles, few but not of definite number, usually three or four, extend the length of the ovule from the end of the original bundle, in the chalaza, nearly to the level of the micropyle.

While the integument is growing up about the nucellus (fig. 18), the meiotic divisions of the nucleus of the megaspore mother cell, and the accompanying cell divisions, begin to take place (figs. 19, 22-24). A T-shaped tetrad of megaspores is produced. The spore at the chalazal end is functional.

The nucleus of the functional megaspore undergoes three successive divisions, while the three non-functional spores and the nucellus are absorbed (figs. 25, 26; the stage with eight free nuclei has not been seen). An embryo sac with an egg and two synergids, two polar nuclei and three antipodal cells, is organized (fig. 27). The antipodal cells appear moribund from the time when they are set apart, and soon disappear. During



FIGS. 22-37. *Fraxinus velutina*: 22, nucellus showing diad cells, $\times 320$; 23, homeotypic metaphase, $\times 320$; 24, tetrad of megaspores, $\times 320$; 25, 2-nucleate embryo sac, $\times 320$; 26, 4-nucleate embryo sac, $\times 320$; 27, mature embryo sac, $\times 320$; 28, fertilization, $\times 320$; 29, first division of endosperm nucleus, $\times 320$; 30, 31, zygote and endosperm in 4-celled stage, $\times 320$; 32, 33, zygote about one month after fertilization, $\times 320$; 34, first division of zygote, $\times 320$; 35, four-celled embryo in many-celled endosperm, $\times 320$; 36, dissection of lower part of fruit about two months after fertilization, $\times 20$; 37, longitudinal section of seed at same stage as in fig. 36, $\times 80$. *h*, hypostase.

the development of the embryo sac, the inner epidermis of the integument takes on the character of a jacket layer.

The meiotic divisions appear always to take place earlier in one of the four ovules of the ovary than in the others (figs. 18, 19 show the beginning of meiosis before the integument is fully developed; figs. 20, 21 show a fully formed ovule in which meiosis has not begun). Through all later stages, one ovule is always found in a more advanced stage of development than the others. More ovules than one may develop complete embryo sacs; pollen tubes may enter more than one ovule; but only the ovule which developed most rapidly is capable of maintaining an embryo. Developed embryo sacs in other ovules undergo degeneration by a process of collapse which begins at the chalazal end.

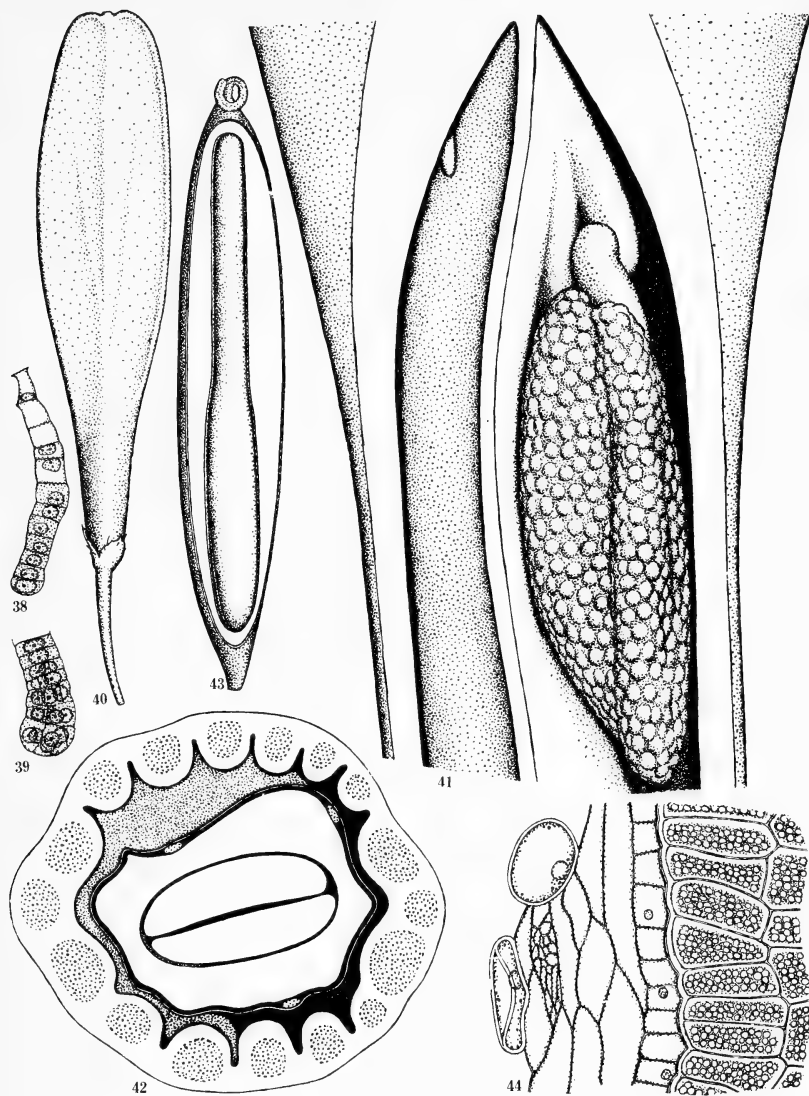
When the embryo sac is ready for fertilization, the ovule contains a hypostase, consisting of a small body of differentiated chalazal cells. It is recognizable by cell walls which are relatively retentive of the dye safranine; in sections stained with haematoxylin alone, it is not recognizable. It is separated from the chalazal end of the embryo sac by a few undifferentiated cells.

FERTILIZATION, ENDOSPERM, AND EMBRYO

Pollen tubes have been seen in the micropyles of various ovules. Their discharged tips, of the form of heavily staining masses, have been seen between pairs of synergids in which the nuclei remain recognizable: it appears that both synergids survive for some time after the entrance of the pollen tube. On several slides, one sperm nucleus has been seen near the egg nucleus, while the other sperm nucleus is in process of fusing with the polar nuclei (fig. 28).

The endosperm is cellular from its origin. The first division of its nucleus (fig. 29) is followed by deposition of a transverse wall. The divisions of its daughter nuclei are followed by the deposition of walls which are transverse or nearly so: the endosperm passes through a stage in which it is a linear (or nearly linear) tetrad of cells (figs. 30, 31). During further multiplication, the cells of the endosperm do not become differentiated except for the crushing of some of them at the micropylar end; no haustoria are produced. The chalazal end of the endosperm digests or crushes the cells of the chalaza as far as the hypostase. For the rest, the endosperm does not digest the adjacent cells. It appears to press upon the jacket layer and the hypostase, and the integument grows along with the endosperm.

Fertilization having taken place early in March, the zygote remains undivided until about the beginning of May, by which time the endosperm is already many-celled. Before the zygote divides, it may become enlarged (figs. 32, 33). After it divides, the enlargement disappears; there is no exceptionally swollen cell at the base of the suspensor (figs. 34, 35). Dividing transversely, the zygote and its progeny produce a uniseriate filament of a dozen or more cells (figs. 37-39). The definitive embryo



FIGS. 38-44. *Fraxinus velutina*: 38, 39, embryos from same collection as figs. 36 and 37, $\times 320$; 40, mature fruit, $\times 4$; 41, dissection of lower part of mature fruit, $\times 20$; 42, cross section of lower part of mature fruit, $\times 20$; 43, dissection of seed (much longer than the one in fig. 41), $\times 8$; 44, section of outer part of seed, seed coat to the left and endosperm to the right, $\times 320$.

originates by longitudinal divisions in several cells at the distal end of this filament. The proximal cells lose their stainable contents, shrink, and disappear.

FRUIT AND SEED

Between early March and late May, growth of the ovary produces a samara of mature size. There are great differences in rate of growth between different parts of the ovary and different dimensions of the parts. The lower part of the ovary, originally a small moderately flattened cylinder, retains this shape while growing to seven or eight times its original dimensions. The upper part, while undergoing slight increase in thickness, grows to some fifteen times its original width and fifty times its original length. Thus it produces the wing of the samara. The wing is not derived from the style, which persists, if at all, as a withered terminal scrap.

The internal septum of the ovary, originally a wall with nearly plane surfaces, undergoes swelling immediately after fertilization and becomes fusiform. The bundles of the ovary wall become greatly enlarged by the differentiation of masses of fibers and form vertical ribs on the inner surface. Septum and ribs fill the locules, leaving scant clefts of complicated form.

Of the four ovules which are hung from the upper part of the septum, three undergo no growth, but turn dark and shrivel. The fourth develops at its proximal end a long funiculus which holds the main body of the developing seed at about the middle of the height of the septum (fig. 36). During the growth of the funiculus, its surface is thrown into microscopic transverse ridges.

The seed proper, enlarging principally after the beginning of July, reaches dimensions approximately half of those of the lower part of the fruit, that is, of the fruit apart from the wing (fig. 41). In the course of this growth, the seed presses into, and largely crushes, the enlarged septum. It pushes back the funiculus, throwing it into coils. The surface of the mature seed is yellow to brown, shiny, and minutely papillate.

Dissection shows the seed to have a thin coat covering an endosperm in which lies a large cylindrical embryo divided through the distal half of its length into two cotyledons (figs. 42, 43). The papillae on the surface of the seed are enlarged epidermal cells. The jacket layer, that is, the internal epidermis of the integument, remains intact. With the exception of the papillae, the jacket layer, and small bodies of fibers in the four or five longitudinal bundles, the cells of the integument are compressed and nearly empty. A definite continuous wall at the outer margin of the endosperm belongs to the endosperm, not to the jacket layer. The cells of the endosperm are packed with granules (fig. 44). These are definitely not of starch; they appear to be of protein.

DISCUSSION

Schnarf's account of the embryology of Oleaceae consisted of scattered observations upon *Forsythia*, *Jasminum*, *Ligustrum*, and *Fraxinus* in the classic general papers of Hofmeister (1858), Warming (1878), Guignard (1882), Billings (1901), Juel (1915), and Dahlgren (1923, 1927). Sommer (1929) had studied *Fraxinus excelsior* among various plants in which

a distinction among the ovules of a single ovary, some continuing their development and others undergoing abortion, appears suddenly at a certain stage of development. Eames (1931) included *Syringa* and *Forsythia* among plants in which he studied the vascular supply of the pistil. Subsequent embryological studies include those of Andersson (1931) on a wide variety of Oleaceae, and of King (1938) and Messeri (1950) on the domestic olive, *Olea europaea*. Johnson (1941) included *Forsythia* among plants in which he studied the cytology of the male gametophyte. Fotidar (1942) studied the floral anatomy of *Nyctanthes*. Numerous counts of chromosomes are reported by Sax (1930), O'Mara (1930), Sax and Abbe (1932), Taylor (1945), and Dutt (1952); the contribution of Taylor is particularly interesting as including counts for *Fraxinus velutina* and its varieties, and as proposing to limit the subfamily Oleoideae to genera in which the basic chromosome number is 23, thus excluding *Jasminum* and *Menodora*.

The observations on *Fraxinus velutina* here presented are in very nearly complete agreement with the facts as to Oleaceae in general as stated in the literature just cited. Andersson noted in various Oleaceae the peculiar tapetum, characteristic of widely scattered presumably derived groups, in which the nuclei divide more than once. Johnson found the pollen grains of *Forsythia* binucleate. The vascular supply of the pistil, alike in *Syringa*, *Ligustrum*, *Nyctanthes*, and *Fraxinus*, exhibits slight variations upon a common pattern which is precisely that of the typical bicarpellate compound pistil according to the theory of Eames. The pattern of the vascular supply to the ovules is identical in *Olea* and *Fraxinus*. Billings was presumably mistaken in describing, in the ovule of *Fraxinus excelsior*, a single vascular strand which descends the raphe to the chalaza and ascends the integument on the side opposite the raphe. In *F. velutina*, as noted, a varying small number of bundles, in positions which vary from one ovule to another, run up from the chalaza; Fotidar observed the same structure in *Nyctanthes*. Also, as Dahlgren suspected, Billings was surely mistaken in figuring an ovule in which the megaspore mother cell is covered by more than one layer of cells of the nucellus: this appearance represents an oblique section of the ovule. In most Oleaceae, the embryo sac is of normal type and the definitive embryo develops from several distal cells of a filamentous early embryo. In these points, *Olea* appears exceptional: its embryo sac is said to be of *Scilla*-type and its filamentous early embryo is very short.

The proper location of Oleaceae in the taxonomic system is next to be discussed. The traditional place of the family is in an order named Contortae. The order was established by Linnaeus (1764) to include the plants subsequently assembled as families Apocynaceae and Asclepiadaceae. Of *Olea* and its allies, Linnaeus made a separate order Sepiariae; he placed *Gentiana* among primulaceous plants in his order Rotaceae. Eichler (1886) and Engler (1892) are responsible for assembling as order Contortae the families Oleaceae, Loganiaceae, Gentianaceae,

Apocynaceae, and Asclepiadaceae. In earlier presentations of the Englerian system, one finds the small tropical family Salvadoraceae placed next to Oleaceae; in later presentations it is dismissed from this neighborhood, surely correctly, since the ovules of Salvadoraceae have two integuments and a nucellus of more than one layer of cells (David, 1938). Wettstein (1908) followed Linnaeus and most pre-Englerian authors in placing Oleaceae in an order (he called it Ligustrales) separate from Contortae. Schnarf followed Wettstein, although expressing doubt that the families remaining in Contortae belong together as a natural group. Wettstein (1908) is authority for family Menyanthaceae, a segregate from Gentianaceae, and Schnarf (1931) is authority for family Buddleiaceae, a segregate from Loganiaceae. Tournay and Lawalrée (1952) transferred Menyanthaceae and Buddleiaceae from Contortae to Ligustrales.

Schnarf, and Tournay and Lawalrée, were influenced by embryological knowledge, including particularly the following point. The endosperm is nuclear in proper Loganiaceae and Gentianaceae, and in Apocynaceae and Asclepiadaceae. It is cellular in Buddleioideae, Menyanthoideae, and Oleaceae.

Assuming that the production of a nuclear endosperm is a primitive character from which the production of the cellular endosperm has repeatedly been derived, the presence of both types in a particular order or family is not by itself sufficient reason for dividing the group. We can interpret Loganioideae, Gentianoideae, Apocynaceae, and Asclepiadaceae as a natural series in which the primitive type of endosperm is retained, and Buddleioideae and Menyanthoideae as offshoots from it in which the derived type of endosperm has developed independently. This appears to be the idea of Moore (1947), who considers Loganiaceae to be an immediate ally or derivative of some primitive stock from which have evolved also the Tubiflorae (among which a repeated evolution of the cellular endosperm is evident) and the Rubiales (which retain the nuclear endosperm).

The Buddleioideae have a cellular endosperm with haustoria (Moore describes these as absent in *Polypremnium*, but one of his figures shows structures to which no other term can be applied) and an embryo developed from two cells terminal upon a three-celled suspensor (Souèges, 1940; Moore, 1948).

Of Menyanthoideae, the writer has learned nothing beyond what was known to Schnarf. A tapetum in which the nuclei divide more than once; an embryo sac of normal type, with fugitive antipodal cells; a cellular endosperm in which cell divisions beyond the first are transverse, and which lacks haustoria; and an early embryo of the form of a many-celled filament: all of these are characters in precise agreement with Oleaceae. To present knowledge it appears probable that the Oleaceae are derived from the Menyanthoideae and should be placed after that group.

SUMMARY

1. *Fraxinus velutina* Torrey, the Arizona ash, a tree of the southwest-

ern United States, is a typical ash of the group having dioecious apetalous flowers. The flowers and their vascular systems are described. The vascular system of the pistillate flower is very nearly that of the typical bicarpellate compound pistil according to the theory of Eames.

2. Staminate flowers consist of little more than two stamens with ribbed endothecia and tapeta in which the nuclei divide more than once and then undergo random fusions. The haploid chromosome number is 23. Pollen grains are 4-grooved, binucleate.

3. The ovules are unitegmic and tenuinucellate. They have several longitudinal bundles in the integument and an obscure hypostase in the chalaza. The inner epidermis of the integument becomes a jacket layer. Of four ovules in the ovary, only one becomes a seed.

4. The embryo sac is of normal type, the antipodal cells disappearing quickly.

5. Double fertilization was observed.

6. The endosperm is of cellular type. The first cell division is by a transverse wall; the second cell divisions are by walls which are transverse or nearly so. No haustoria are produced.

7. The zygote, after remaining undivided for several weeks, produces a filament of many cells. The embryo proper is derived from several cells at the distal end of this filament.

8. The single seed of the samara crowds aside or crushes other structures within the ovary and becomes mature in autumn. Papillae upon its surface are enlarged epidermal cells. The jacket layer persists to this stage. A continuous wall within the jacket layer is the outer cell wall of the endosperm. There is a large straight dicotyledonous embryo.

9. These observations, compared with others in the literature, tend to substantiate the naturalness of the family Oleaceae and the order Contortae. Among other Contortae, the Menyanthoideae appear most similar to Oleaceae in embryological characters.

Sacramento City College
Sacramento 22, California

LITERATURE CITED

- ANDERSSON, A. 1931. Studien über die Embryologie der Familien Celastraceae, Oleaceae und Apocynaceae. Lunds Univ. Årskr. n. f., Avd. 2, 27, no. 7: 1-110.
- BILLINGS, F. H. 1901. Beiträge zur Kenntniss der Samenentwicklung. Flora 88: 253-318.
- DAHLGREN, K. V. O. 1923. Notes on the ab initio cellular endosperm. Bot. Notiser 1923: 1-24.
- . 1927. Die Morphologie der Nuzellus mit besonderer Berücksichtigung der deckzellosten Typen. Jahrb. wiss. Bot. 67: 347-426.
- DAVID, ELISABETH. 1938. Embryologische Untersuchungen an Myoporaceen, Salvadoraceen, Sapindaceen und Hippocrateaceen. Planta 28: 680-703.
- DUTT, M. 1952. Chromosome numbers in some ornamental jasmines. Science and Culture 17: 527-528.
- EAMES, A. J. 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. Jour. Bot. 18: 147-188.
- EICHLER, A. W. 1886. Syllabus der Vorlesungen über spezielle und medicinisch-pharmaceutische Botanik. 4th ed. Berlin.

- ENGLER, A. 1892. Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik. Berlin.
- FOTIDAR, A. N. 1942. Floral anatomy of *Nyctanthes Arbor-tristis* L. Jour. Indian Bot. Soc. 21:159-166.
- GUIGNARD, L. 1882. Recherches sur le sac embryonnaire des phanérogames angiospermes. Ann. Sci. Nat. Bot. sér. 6, 13:136-199.
- HOFMEISTER, W. 1858. Neuere Beobachtungen über Embryobildung der Phanerogamen. Jahrb. wiss. Bot. 1:82-188.
- JOHNSON, G. W. 1941. Cytological studies of male gamete formation in certain angiosperms. Am. Jour. Bot. 28:306-319.
- JUEL, H. O. 1915. Untersuchungen über die Auflösung der Tapetenzellen in den Pollensäcken der Angiospermen. Jahrb. wiss. Bot. 56:337-364.
- KING, J. R. 1938. Morphological development of the fruit of the olive. Hilgardia 11:437-458.
- LINNAEUS, C. 1764. Genera plantarum. . . 6th ed. Stockholm.
- MESSERI, ALBINA. 1950. Alcuni dati sulla embriologia ed embriogenesi di "*Olea europaea*" L. Nuov. Giorn. Bot. Italiano 57:149-169.
- MOORE, R. J. 1947. Cytotaxonomic studies in the Loganiaceae. I. Chromosome numbers and phylogeny in the Loganiaceae. Am. Jour. Bot. 34:527-538.
- . 1948. Cytotaxonomic studies in the Loganiaceae. II. Embryology of *Polypremum procumbens* L. Am. Jour. Bot. 35:404-410.
- MUNZ, P. A. and J. D. LAUDERMILK. 1949. A neglected character in western ashes. El Aliso 2:49-62.
- O'MARA, J. 1930. Chromosome number in the genus *Forsythia*. Jour. Arnold Arb. 11:14-15.
- PRATT, M. B. 1922? Shade and ornamental trees of California. Sacramento?
- SAX, K. 1930. Chromosome number and behavior in the genus *Syringa*. Jour. Arnold Arb. 11:7-14.
- and E. C. ABBE. 1932. Chromosome numbers and the anatomy of the secondary xylem in the Oleaceae. Jour. Arnold Arb. 13:37-48.
- SCHNARF, K. 1931. Vergleichende Embryologie der Angiospermen. Berlin.
- SOMMER, BERTA-SIBYLLE. 1929. Über Entwicklungshemmungen bei Samenanlagen. Flora 124:63-93.
- SOUÈGES, R. 1940. Embryogénie des Loganiacées. Développement de l'embryon chez le *Buddleia variabilis* Hemsley. Compt. Rend. 211:139-140.
- TAYLOR, H. 1945. Cyto-taxonomy and phylogeny of Oleaceae. Brittonia 5:337-367.
- TOURNAY, R., and A. LAWALRÉE. 1952. Une classification nouvelle des familles appartenant aux ordres des Ligustales et des Contortées. Bull. Soc. Bot. France 99:262-263.
- VON WETTSTEIN, R. 1901-1908. Handbuch der systematischen Botanik. 2 vols. Leipzig and Vienna.

A NEW SILENE FROM NORTHWESTERN CALIFORNIA

A. R. KRUCKEBERG¹

Long past is the era in California botany when a collector could count among his season's haul a good proportion of undescribed species. Most areas of the state are sufficiently well known so as to limit the likelihood of uncovering anything new. Nowadays, range extensions, records of new adventives, and the discovery of some inconspicuous annual that fails to

¹ Supported by funds from the State of Washington Initiative No. 171 and by the National Science Foundation, Grant G-1323.

match any known relative, serve to satisfy the field botanist's taste for novelties. When a hitherto undescribed perennial which is an element of a stable plant community is found, it is of more than passing interest. Such discovery is most likely in the relatively little explored mountainous terrain of northwestern California. *Silene marmorensis* Kruckeberg, described below, is one of these latter day discoveries, having been collected in 1954 by Dr. C. Leo Hitchcock along the forested slopes of the Marble Mountains in southwestern Siskiyou County.

For the past eight years, I have been maintaining a collection of living plants of North American species of *Silene*. The plants have been grown for purposes of observation under uniform conditions, for determining chromosome number (Kruckeberg 1953, 1960), and for assessing degree of genetic relationships by means of interspecific hybridization (Kruckeberg 1954). The genus is represented in California by twenty native species (*sensu* Hitchcock and Maguire 1947), nearly all of which are well represented in herbaria. Moreover, most of them are readily distinguishable and thus stand out as clearly defined species. Having worked with living plants of all the Californian species as well as most of the known species occurring elsewhere in North America, I was genuinely impressed with a specimen that did not fall into place with any known species.

In general habit, *Silene marmorensis* might be confused with the Sierra Nevada *S. verecunda* Wats. subsp. *platyota* (Wats.) H. & M., both having long, flexuous stems and short, lanceolate leaves. In inflorescence and floral characters, though, the new species combines features of at least three species—*S. campanulata* Wats., *S. lemmonii* Wats., and *S. bridgesii* Rohrb.—all of which share, as well, the common characteristics of an ovoid, cartilaginous capsule and large black seeds; in addition, all four species are tetraploid ($2n = 48$). The new species appears most closely related to *S. bridgesii* of the yellow pine belt in the Sierra Nevada, owing to the close correspondence of the two species in inflorescence and flowers. However, in *S. marmorensis*, the flowers are not pendant, nor do the proportions of its calyx, petals, and style match those of *S. bridgesii*.

The suite of characters which defines *S. marmorensis* can be summarized as follows. The several wiry, weakly ascending stems bear 5–7 pairs of uniformly short, lanceolate leaves; the open, lax, glandular inflorescence bears 4–6 pairs of lateral cymules, with the cymules consisting of single flowers in wild plants and the lateral flowers apparently abortive; the flowering calyces are elongate, ovate-lanceolate, and are borne divaricately on thin, wiry pedicels. The pinkish petals have a simple, bifid blade at the base of which are the two laterally divaricate, erose auricles; the appendages are short and rather broad. No one of these features is specific for a western *Silene*, but in ensemble, they contrive to give a picture of a rather delicate, unassuming grace and uniqueness to the plant (figs. 1–3).

Having examined only two collections of *S. marmorensis*, it would be rash to attempt a delimitation of its distribution and habitat preference.

The two specimens cited below were collected along the steep, winding forest road leading northeast up to Camp Three from the confluence of the Salmon and Klamath rivers at Somes Bar. The terrain is steep, forested mountainside with a south to southwest exposure. A topotype collection (*Kruckeberg 4023*) grew in loose talus of gabbroic rock in a fairly open stand of Douglas fir, black oak, and madrone. A list of associated species is appended to the species description.

***Silene marmorensis* sp. nov.**² *Planta perennis tenui radice; caudice caulibus compluribus tenuibus, 2.5–4.0 dm. longis, puberulentis, supra glandulosis; foliis caulinis 5–7 paribus, fere eadem magnitudine, lanceolatis, 3.0–4.5 cm. longis, 0.3–0.5 cm. latis, scabrido-pubescentibus; bracteis reductis, lineari-lanceolatis, glandulosis; inflorescentibus terminalibus, 10–20 cm. longis, fere simplicibus, cymulis 5–7 iugis, pedicellis 7–10 mm. longis, filiformibus, glandulosis; calyce 13 mm. longo, anguste elongato-ovato, glanduloso, minus valide 10-nervo, lobis late lanceolatis, 3 mm. longis; calyce in fructu campanulato; corolla supra ex rubro pallea, infra subviridilurido (galbino), ungue 8–10 mm. longo, glabrato, sursum latiore, auriculo parvo eroso in utroque summae latere, lamina 4–6 mm. longa oblongata, alte bilobata, lobis integris vel in apice tenuiter erosis, appendicibus 2, oblongatis; staminibus exsertis, in tubo compressis, filamentis 11–13 mm. longis, glabratis, polline subfusco; stipitibus 3–4 mm. longis, puberulentis; stylis 3, 10–12 mm. longis, filiformibus, papillis stigmatum paucis et tantummodo in apice styli; ovariis glabratis ovatis maturitate et ligno-cartilagineis et 5-dentatis; seminibus 2.5 mm. longis, nigris, fulgentibus, tuberculis ex ordinibus brevibus conicis.*

Perennial, from a long slender taproot, the multicapital crown bearing several underground, erect branches, each of which terminates above ground in a slender stem, 2.5–4.0 dm. long, stems simple, purplish and eglandular-pubescent at base, retrorsely glandular-pubescent above, especially on branches of inflorescence; the 5–7 pairs of cauline leaves similar in size and shape, reduced only in the inflorescence, lanceolate, 3.0–4.5 cm. long, 0.3–0.5 cm. wide, sparsely scabrid-pubescent on both surfaces, the leaf-like bracts of inflorescence progressively reduced upwards, short-lanceolate, glandular; inflorescence terminal, 10–20 cm. long, simple, or with 1–2 branches, each bearing 5–7 pairs of cymules (the lateral flowers of each cymule apparently abortive in field material); pedicels 7–10 mm. long, filiform, glandular; calyx in flower indistinctly 10-nerved, glandular, narrowly elongate-ovate, slightly constricted at base, about 13 mm. long, becoming campanulate through distension by the maturing ovary, the teeth ovate-lanceolate, short-acuminate, 3 mm. long, somewhat membranous in the sinuses, margins of teeth densely long-ciliate; corolla pale pink above, greenish yellow beneath, the claw 8–10 mm. long, glabrous throughout, slender at base widening above, with a small erose, angular auricle at either side of summit, the blade 4–6 mm. long, oblong, bilobed

² The Latin diagnosis kindly prepared by W. M. Read, Professor of Classics, University of Washington.



FIG. 1. Type specimen of *Silene marmorensis*, Hitchcock 20221 (WTU 179156), $\times \frac{1}{8}$.

over one-half its length, the lobes oblong, entire to slightly erose at tip, appendages two, broadly oblong, truncate, the free margins entire; stamens slightly exserted, crowded at throat, the filaments 11–13 mm. long, glabrous throughout; pollen tawny brown in color; carpophore 3–4

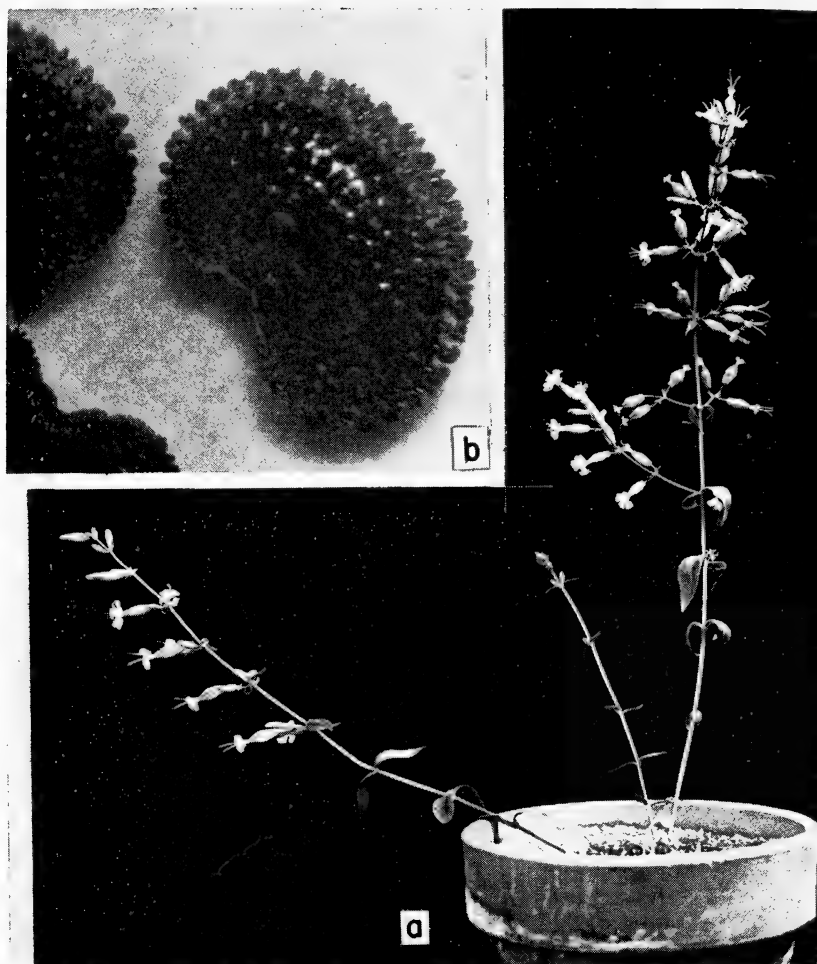


FIG. 2. *Silene marmorensis*: a, plant grown in greenhouse (photo by W. Martin, Still Photo Unit, University of Washington); b, seed, \times ca. 20.

mm. long, retrorsely puberulent; styles three, 10–12 mm. long, filiform, nearly straight, the stigmatic papillae few and congested at tip; ovary glabrous, at maturity ovoid with walls woody-cartilaginous, opening with five teeth; seeds about 2.5 mm. long, black, shiny, with concentrically longitudinal rows of short conical tubercles. $2n = 48$. Figs. 1–3.

Type. Siskiyou County, California: 1.0 mile north of Somes Bar on road to Camp Three, June 22, 1954, *C. L. Hitchcock* 20221 (WTU 179156); another specimen (topotype) from 5.5 miles above Somes Bar on road to Camp Three, growing in loose talus of gabbroic rock, *A. R. Kruckeberg* 4023 (WTU 172672). Some of the vegetation associated with *Kruckeberg* 4023 is as follows: *Pseudotsuga menziesii*, *Quercus*

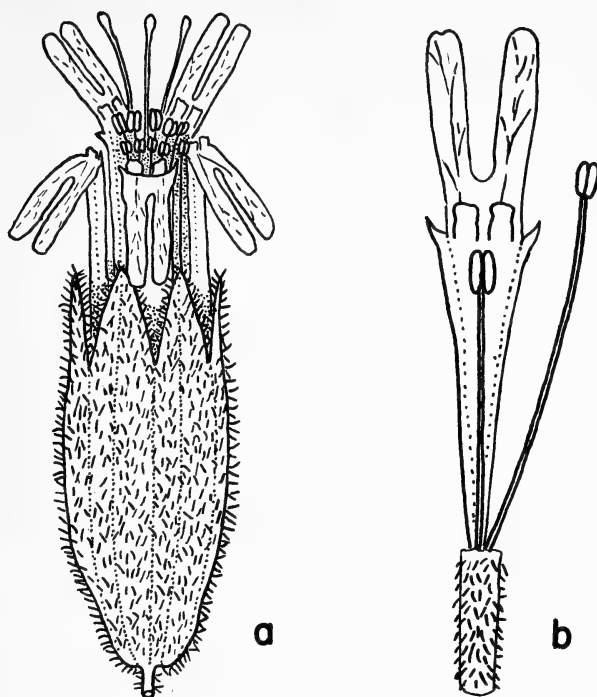


FIG. 3. Flower of *Silene marmorensis*: a, single whole flower; b, carpophore with attached single petal and stamen. All $\times 7$.

kelloggii, *Arbutus menziesii*, *Cornus nuttallii*, *Quercus chrysolepis*, *Acer macrophyllum*, *Pinus lambertiana*, *P. ponderosa*, *Lithocarpus densiflora*, *Corylus californica*, *Ceanothus integerrimus*, and *Cercis occidentalis*; also a sparse covering of such herbaceous plants as *Cynoglossum occidentale*, *Poa* sp., *Galium* sp., *Stephanomeria* sp., *Polystichum lemmonii*, *P. munitum*, *Pteridium aquilinum*, *Hieracium albiflorum*, *Eriophyllum lanatum*, *Iris* sp., and *Smilacina racemosa*.

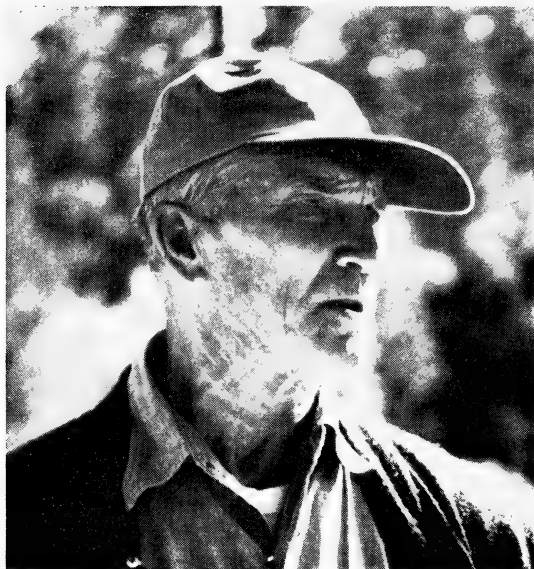
Department of Botany,
University of Washington,
Seattle 5, Washington

LITERATURE CITED

- HITCHCOCK, C. L. and B. MAGUIRE. 1947. A revision of the North American species of *Silene*. Univ. Wash. Publ. Biol. 13: 1-73.
KRUCKEBERG, A. R. 1954. Chromosome numbers in *Silene* (Caryophyllaceae): I. *Madroño* 12: 238-246.
———. 1955. Interspecific hybridizations of *Silene*. *Am. Jour. Bot.* 42: 373-378.
———. 1960. Chromosome numbers in *Silene* (Caryophyllaceae). II. *Madroño* 15: in press.

FREED HOFFMAN

1880-1959



The botanical career of Mr. Freedom W. Hoffman, who died at his home near Guerneville, California, 13 November 1959, spanned a fifty-year period. Freed was born at Knights Landing, Yolo County, 30 January 1880, where he lived until he went away to school at about the age of fifteen. As his mother was of French descent, Freed learned, as a child, to speak French and he retained his fluency and interest in this language throughout his life. Following his graduation from Chico Normal School he studied art in New York City for several years. Upon his return to California he began a teaching career in which he achieved considerable success for something over a decade.

On 24 August 1907, Freed married Jemella Gertrude Peugh. Throughout the forty-seven years of their married life, Jimmy regularly accompanied Freed on trips into the remote back country. In the early days such trips were made with burro or mule, while later a Jeep served a similar purpose.

While at Berkeley soon after his marriage, Freed became principal of the LeConte School, to which he often referred in later years as the first Junior High School in America. At about this time Freed studied with Professor Setchell and Professor Gardner in the Botany Department at the University of California at Berkeley. He mentioned to me several times Dr. Gardner's offer of a teaching assistantship which, while it tempted him, was rejected in favor of a teaching position at San Francisco Normal School.

I first met Freed and Jimmy at their home near Guerneville in the early summer of 1941. Freed had sent some interesting specimens of *Streptanthus* to the Herbarium at the University of California, Berkeley, for identification. In order to meet the collector and see the populations of plants, I drove to Guerneville. From the beginning of our eighteen-year friendship I was charmed by Freed. His slow, patient, deliberate approach to problems made a real impression on me.

Because I was interested in *Streptanthus* and its distribution in relation to serpentine soils, because I enjoyed being with Freed and Jimmy, and because I could collect abundant fresh flowering plant material near Guerneville for class use, I went back to the Hoffmans' several times during the summer of 1941. On one occasion Freed and I spent several days beginning the construction of a cabin on a remote hunting claim, which Freed had proven to be still part of the public domain in 1910 and 1911 even though it had previously changed hands several times in land deals. Careful search of land office records and many weekends spent surveying had finally enabled him to file on the quarter section as a hunting claim. Its chief value lay in the existence of a spring not far below a ridge top. Freed and I hunted deer, fruitlessly, in the early mornings and the early evenings. During the day we began a cabin to replace the old one built by Freed in 1911. As we leisurely cut and notched the sill logs, Freed recounted, interspersed with discussions of the Pythagorean theorem, his reasons for leaving teaching to become an orchardist.

Freed Hoffman was a man with a very considerable artistic talent. His oils and watercolors with which their home and guest cottage were hung made a lasting impression on all who saw them. The intricate woodcarving on the massive lauan loom which he built for Jimmy was still another evidence of his creative ability. As a carpenter, stone mason, botanist, botanical artist, Freed's accomplishments were of professional quality. Certainly his abilities as a teacher were equally great. Yet he resigned his teaching position, left a career for which he seemed well fitted, and still in his thirties, took over the management of the extensive orchards owned by himself and Jimmy near Guerneville.

With brush and palette, with hammer and saw, with pruning hook and picking basket and ultimately with plant press and seed bed, Freed found that he could see and sense the results of his labors almost immediately, while in teaching often many years passed before results were evident. Freed had the kind of patient sensitivity that would lead him to cut down his fruit picking speed by half in order not to discourage completely a youngster during his first day on the ladder, but he simply could not wait the many years to be greeted by a former pupil, now a mature man, who might say, "You probably don't remember me, Professor Hoffman, but you taught me geometry. . . ."

With the realization in 1941 that serpentine outcroppings often supported unusual populations of plants, Freed began a series of botanical trips which eventually brought his collections over the 4000 mark. Among

his collections from remote and little-known serpentine areas is the type specimen of *Haplopappus ophitidis* (J. T. Howell) Keck. An *Allium* collected by Freed is likely to be the type of a new species. Especially in the genus *Streptanthus*, in which he published two new species in 1952, Freed's numerous collections have increased greatly our knowledge of variation and geographic distribution.

When World War II ended and gasoline, as well as new vehicles, became readily available, Freed purchased a Jeep in which he and Jimmy traveled widely in search of serpentine and "Streps." Jimmy's death in June, 1953, following their return from an extensive collecting trip in the Southwest, was a blow from which Freed found it almost impossible to recover. A trip to the Piedmont of North Carolina to visit Jimmy's relatives and the thoughtful solicitude of friends finally restored in Freed his former interests.

On 7 April 1955 Freed married Blanche Lenora Griden, who survives him. Blanche's lively interest in Freed's botanical studies and her devoted care during the trying time of Freed's stroke and his lengthy and arduous convalescence have endeared her to those of us who came to know her through Freed.

Freed's ties with the profession of botany were primarily with members of the California Botanical Society and the personnel of the Herbarium at Berkeley. He corresponded rather regularly with Bacigalupi, Carter, Kruckeberg, McMillan, Mason, Morrison, and others interested in serpentine, *Streptanthus*, or both. His collections, his watercolor sketches, especially of *Streptanthus*, and his voluminous notes on various sections of this genus are on deposit in the Herbarium of the University of California at Berkeley.—JOHN L. MORRISON, State University, College of Forestry, Syracuse University.

CLEARED CARDIOCARPON LATE-ALATUM LESQ., CORDAITEAN SEEDS FROM MICHIGAN¹

J. F. DAVIDSON

Arnold (1948) described *Spermatites cylix* from the Big Chief No. 8 mine at St. Charles, Michigan, as appearing to be the apical portion of a very large spore. The present account may throw some light upon the nature of the object so designated, while extending our knowledge of the material previously identified (Arnold, 1949) as *Cardiocarpon late-alatum* Lesq.

The Cordaitean seed that Lesquereux described as *Cardiocarpon late-alatum* (1879, Pl. LXXXV, figs. 46, 47; 1880, p. 568) is a small, rounded, slightly cordate body, about 9 mm. wide and 10 mm. long. The nucule,

¹ This work was financed in part by a grant from the University of Nebraska Research Council.

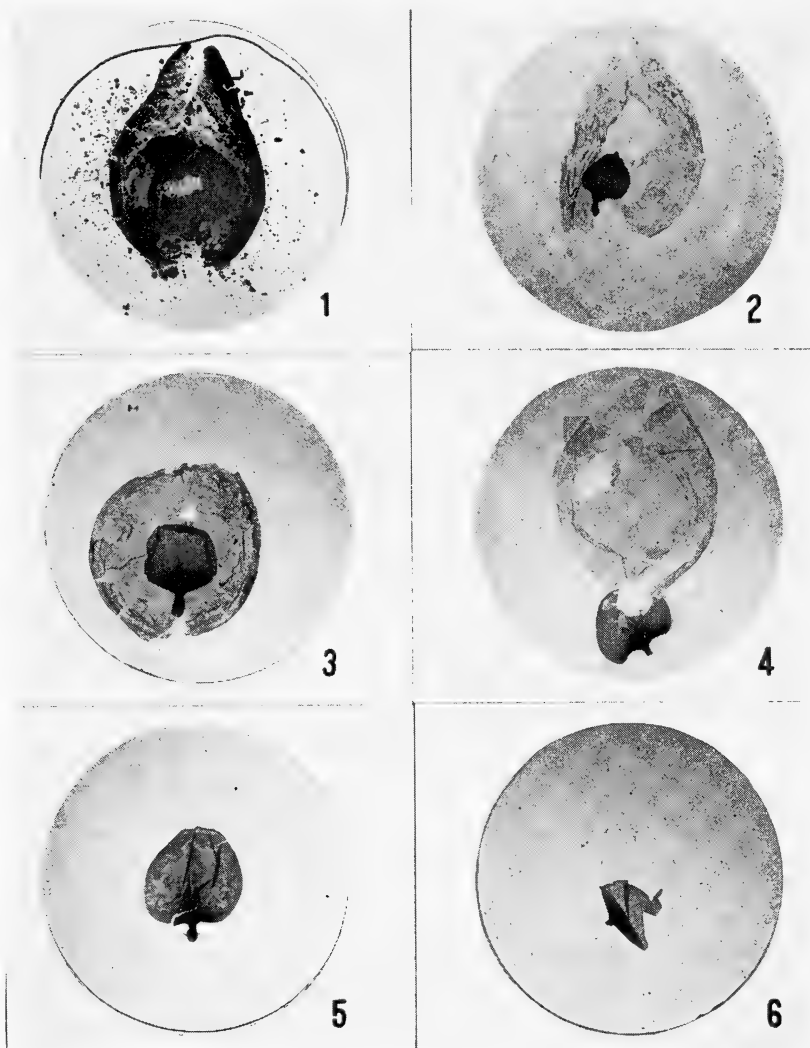
as figured, is about 5 mm. wide, and is surrounded by a marginal wing which varies from 2 to 3 mm. in width. The apical portion of the wing is only slightly prolonged. Lesquereux expressed uncertainty about the validity of the distinction between this species and *C. zonulatus* and *C. simplex*, all three being from the sub-conglomerate at Pittston, by saying: "Perhaps these three forms, separated as species, represent the same, although the differences appear evident" (1880, p. 569). Of these three species, however, the specimens from Grand Ledge, Michigan, which are discussed below, show the closest resemblance to Lesquereux' figures 46 and 47 which represent *C. late-alatum*. While Lesquereux was familiar with Brongniart's work in which the name *Cardiocarpon* was used for silicified seeds, he based his own separations on characters expressed in compressions.

In 1955, large numbers of *Cardiocarpon* seeds were collected at Grand Ledge, Michigan. These occurred in the shale immediately below what Kelly (1933) designated as "Cycle A" in his Pennsylvania stratigraphy. In the dried shale, the seeds could be studied only as compressions, but when freshly-collected shale was submerged in water the shale immediately started to disintegrate and some of the seeds, as well as other plant remains, could be recovered.

An attempt to clear the seeds with concentrated nitric acid and potassium chlorate (Schultz's solution) and 1 per cent ammonium hydroxide resulted in quite opaque preparations (fig. 1). This was apparently due to the intrusion of shale within the layers of the integument, and was eliminated by soaking the seeds in hydrofluoric acid previous to clearing. Such seeds were dehydrated in alcohol before mounting permanently in Diaphane.

In addition to the more or less complete seeds, several other isolated fragments were cleared. Some of these fragments were portions of the nucellar region of the seed, which showed no evidence of the previously-surrounding integument tissue. During the clearing and mounting process, the nucellar portions showed a strong tendency to become separated from their enveloping integuments. Since the cuticle of the integument is more delicate than that of the nucellus, it is logical that the latter would be occasionally preserved after the disintegration of the surrounding integument.

With the variation evident in these seeds, together with the variation originally recognized by Lesquereux, we are faced with two alternatives as regards the disposition of the specimens within our nomenclatural system. If we accept the names proposed by Lesquereux as denoting three species of Paleozoic seeds, then we can validly apply his names only to those specimens which agree exactly with his figured and described types. This implies that the vast majority of specimens which do not so agree will have to be described as new species. This might well be the case here. The alternative deals with probabilities. Since Lesquereux stated that his specimens from the same habitat were *possibly* conspecific, and since



FIGS. 1-6. *Cardiocarpon late-alatum* Lesq. (Circles are 18 mm. in diameter.) FIG. 1. Mature seed. (Without treatment with hydrofluoric acid, the intruded shale obscures detail. Other figures are cleared after treatment with hydrofluoric acid. Figures 2-5 show gradually increasing size of nucellus). FIG. 2. Nucellus, although displaced in clearing, shows apical beak. FIG. 3. Nucellus in position. FIG. 4. Displaced nucellus, showing heavily cutinized basal region. FIG. 5. Nucellus found free in the shale. The integument was not preserved. FIG. 6. Portion of the base of a nucellus, found free. (This is the kind of structure described as *Spermatites cylix* Arnold, the type of which was studied in comparison.)

comparable material has been found in another single habitat at Grand Ledge, it is *probable* that the variations encountered represent slight differences in the preservation process, and differences in the ages of the seeds when shed. The latter point is illustrated in the figures, which show variation not only in the over-all size of the seeds, but also in the size of the nucellar region. Were abortion involved, one might reasonably expect to find a series of small, aborted seeds and another series of more or less mature seeds, without the intermediate sizes.

Of the foregoing alternatives, the latter appears the more logical, and less apt to result in a confusion of names. In the material collected at Grand Ledge, some of which is figured here, it is assumed that the variation encountered represents differences in the maturity of individual seeds, and differential preservation of conspecific material. Thus it is here all referred to *Cardiocarpon late-alatum* Lesq.

The seeds from Grand Ledge are flattened, circular to ovate in outline, 9–15 mm. long by 9–11 mm. broad. The basal region shows an indentation at the point of attachment, which extends almost to the swollen basal stalk of the nucellus, while the distal end appears as a deeply bifid beak. The surface of the integument appears to be composed of roughly isodiametric cells, approximately 45 microns in diameter, except for those of the wing, which are about 20–25 microns broad and 60–100 microns long. The wing starts as a narrow band about 0.5 mm. wide near the base of the seed, and gradually increases in width upward to an observed maximum of 2.0 mm. In these specimens, the integuments, with the exception of the wings, were filled with clay, apparently bound with silica, since hydrofluoric acid dispersed it.

The nucellar body is very heavily cutinized, ovoid to globose, 2–7 mm. long, and equally broad. At the proximal end, a compact tissue of heavily-walled cells forms a saucer-shaped base (figs. 4, 5) which in turn arises from a short, 1 mm. long cylinder of similar cells in which no vascular tissue is apparent. The base of this cylindrical stalk is somewhat swollen, the cell walls are thinner, the cells are slightly larger and have a glandular appearance. The tendency for the nucellar portion to separate from the integument is shown in figures 2 and 4, while figure 5 shows the heavily cutinized base of the nucellus beginning to break away from the upper portion, in a specimen found without the surrounding integument. In figure 5 also may be seen the region of attachment of the nucellar stalk to the integument. Figure 6, which is one of the fragments found in the shale and cleared, is merely the basal portion of the nucellar region of a seed.

Although the apex of the nucellar body appears to be rounded in most specimens, closer examination shows that the specimens are incomplete. The smallest (fig. 2) and the largest (fig. 1) individuals show a definite attenuation at the apex such as might be expected to lead to a pollen chamber.

The specimen shown in figure 6 was compared with the type material

of *Spermatites cylis* Arnold, and they appear to be conspecific. Hence, *Spermatites cylis* probably refers to the basal portion of a nucellus from a Cordaitan seed comparable to *Cardiocarpon late-alatum*.

Department of Botany,
University of Nebraska, Lincoln

LITERATURE CITED

- ARNOLD, C. A. 1948. Some cutinized seed membranes from the coal-bearing rocks of Michigan. Bull. Torrey Club 75: 131-146.
———. 1949. Fossil flora of the Michigan coal basin. Contr. Mus. Paleont. Univ. Mich. 7: 131-269.
KELLY, W. A. 1933. Pennsylvania stratigraphy near Grand Ledge, Mich. Journ. Geol. 41: 77-89.
LESQUEREUX, L. 1879. Atlas to the coal flora of Pennsylvania. Second Geol. Surv. Pa. Harrisburg.
———. 1880. Coal flora of Pennsylvania. Second Geol. Surv. Pa. Harrisburg.

THE BASIC CHROMOSOME NUMBER OF THE GENUS NEPTUNIA

(LEGUMINOSAE-MIMOSOIDEAE)

B. L. TURNER AND O. S. FEARING

The genus *Neptunia* is composed of about ten or eleven species of annual and perennial herbs. Its members are widely distributed in the tropical and subtropical regions of the world. Five species are endemic to the Old World (three in Australia, two in India); two are cosmopolitan, occurring in wet habitats, principally in tropical regions; and three or four are confined to North and South America.

The region with the greatest number and diversity of taxa appears to be Texas and adjacent Mexico where four or five species are represented (Turner, 1951). From a standpoint of floral morphology, this area also retains one of the least modified species in the genus (*Neptunia lutea*)¹.

The first chromosome count reported for a species of the genus was by Dnyansagar (1952). He reported a number of $n = 18$ from sectioned anther material of the Indian species, *N. triquetra*. However, the camera lucida drawing documenting this count appears to show 18 somatic chromosomes and is perhaps but a portion of the complement of a single somatic cell of premeiotic "mother cell" tissue.

Turner and Beaman (1953) reported counts for three unnamed American taxa of *Neptunia* as $2n = 28$. Their counts were obtained from somatic cells of sectioned root tip material. The only other report for the genus has been that of Frahm-Leliveld (1953) who listed an approximate

¹ All of the described taxa in the genus, except this species, have some flowers with anantherous stamminodia modified into petaloid structures. *N. lutea* has flowers with the stamens all alike and anther-bearing.

TABLE 1. SPECIES OF NEPTUNIA EXAMINED FOR CHROMOSOME NUMBER

Species	Seed Source and Voucher Collection	Chromosome Number
* <i>Neptunia dimorphantha</i> Domin	AUSTRALIA (Seed communicated by Div. of Plant Industry, C.S.I.R.O., Canberra City). <i>Q227</i>	$2n = 28$ (fig. 3)
* <i>Neptunia gracilis</i> Benth.	AUSTRALIA (As above) <i>C884</i>	$2n = 56$
* <i>Neptunia monosperma</i> Benth.	AUSTRALIA (As above) <i>W652</i>	$2n = 28$ (fig. 2)
<i>Neptunia plena</i> (L.) Benth.	INDONESIA (Reported by Frahm-Leliveld, 1957)	$2n = 78?$
<i>Neptunia triquetra</i> Benth.	INDIA (Reported by Dnyansagar, 1952).	$n = 18?$
* <i>Neptunia prostrata</i> (Lam.) Baill.	INDIA. Raipur (Seed communicated by Dr. V. R. Dnyansagar). <i>Turner s.n.</i>	$2n = 56$ (fig. 1)
* <i>Neptunia lutea</i> (Leavenw.) Benth.	TEXAS. Galveston County: <i>Turner 2189</i>	$2n = 28$ (fig. 5)
* <i>Neptunia lutea</i> (Leavenw.) Benth.	TEXAS. Galveston County: <i>Turner 2923</i>	$2n = 28$
* <i>Neptunia pubescens</i> var. <i>floridana</i> (Small) Turner	TEXAS. Galveston County: <i>Turner 2194</i>	$2n = 28$
* <i>Neptunia pubescens</i> var. <i>lindheimeri</i> (B. L. Robinson) Turner	TEXAS. San Patricio County: <i>M. C. Johnston 541338</i>	$2n = 28$ (fig. 4)

* Indicates new report for the genus.

count for *N. plena* as $2n = \pm 72$; in a later paper Frahm-Leliveld (1956) in reporting the same species, apparently settled on the number $2n = 78$, though the drawing documenting this count is not easily interpreted.

Because of the differing base numbers for the genus reported by these workers, and because of the known unibasic nature of most genera in the Leguminosae, the present authors have reinvestigated the previous reports for the taxa reported by Turner and Beaman and in addition have investigated four species previously unreported.²

MATERIALS AND METHODS. Chromosome counts listed as new in the present paper (Table 1) were made from root tip cells of germinating seeds using a squash technique outlined by Turner and Fearing (1959). Polyploid cells were noted in the tissue of all the taxa examined, though diploid cells appeared to be more common and this is the number given in Table 1.

RESULTS AND DISCUSSION. Altogether, counts for eight of the approximately ten species in the genus have been reported (Table 1). Except for the doubtful count of $n = 18$ for *N. triquetra* and the count of *N. plena*

² Attempts to obtain seed of the controversial *N. triquetra* have been unsuccessful. The authors are grateful to Dr. V. R. Dnyansagar who so kindly furnished the seed of *N. prostrata* used in the present study.



FIGS. 1-5. Camera lucida drawings of the mitotic chromosomes in *Neptunia* spp.: 1, *N. prostrata* ($2n = 56$); 2, *N. monosperma* ($2n = 28$), late metaphase, 2 pair of chromosomes have already separated and are shown in the "unpaired" condition; 3, *N. dimorphantha* ($2n = 28$); 4, *N. pubescens* var. *lindheimeri* ($2n = 28$), prophase; 5, *N. lutea* ($2n = 28$). (\times ca. 1200.)

($2n = 78$), all reported counts have been on a base of $x = 14$. The species here reported are from taxa occurring on several continents, and one of them, *N. lutea*, has a "primitive" floral structure and occurs in a region where several diverse taxa are found. These facts make a base number of $x = 14$ for the genus seem more plausible than that of a multibasic pattern, particularly since *N. triquetra* and *N. plena* are not especially different morphologically from species with known counts of $2n = 28$. In addition it might be noted that related genera of the tribe Adenanthereae, in which *Neptunia* is usually included, are also on a base of $x = 14$ (e.g. *Prosopis* and *Dichrostachys*, Darlington and Wylie, 1956).

SUMMARY

Chromosome numbers for six species of *Neptunia*, all on a base of $x = 14$, are presented for the first time. These counts were obtained from diverse species which occur naturally in Australia, India and Texas. In view of the known constancy of base numbers for most genera of the Leguminosae, and in view of the poor documentation for differing base

numbers reported by other workers, it has been concluded that $x = 14$ is probably the correct base chromosome number for the genus.

The Botany Department, and
Plant Research Institute,
University of Texas, Austin

LITERATURE CITED

- DARLINGTON, C. D., and A. P. WYLIE. 1956. Chromosome atlas of flowering plants. MacMillan Co., New York. 519 pp.
- DNYANSAGAR, V. R. 1952. Embryological studies in the Leguminosae. IV. A contribution to the embryology of *Neptunia triquetra* Benth. Indian Acad. Sci. Proc., Sect. B. 36: 1-11.
- FRAHM-LELIVELD, J. A. 1953. Some chromosome numbers in tropical leguminous plants. *Euphytica* 2: 46-48.
- . 1957. Observations cytologiques sur quelques Légumineuses tropicales et subtropicales. *Rev. Cytol. et Biol. Veg.* 8: 273-287.
- TURNER, B. L. 1951. Revision of the United States species of *Neptunia* (Leguminosae). *Am. Midl. Natur.* 46: 82-92.
- , and J. H. BEAMAN. 1953. Chromosome complements in *Desmanthus* (Leguminosae). *Field and Lab.* 21: 47-50.
- , and O. S. FEARING. 1959. Chromosome numbers in the Leguminosae. II. African species, including phyletic interpretations. *Am. Jour. Bot.* 46: 49-57.

HYBRIDIZATION AND INSTABILITY OF YUCCA

JOHN MILTON WEBBER¹

The contention that hybridization is largely responsible for the widespread variability of southwestern yuccas (2,4,9)² is supported by the following facts. 1) Cross-pollination is enhanced by the yucca's dependence upon the yucca moth for pollination. 2) Two or more species frequently occur in mixed stands or near each other. 3) The karyotypes of all species are strikingly similar (cf. 1). 4) Inter- and intra-specific pollinations produce equally abundant seed. 5) There is little difference in the degree of relationship and the ability to hybridize. 6) Many variants exhibit specific characteristics of two or more species. 7) Apparent hybrids are frequently more fertile than "typical" species. 8) Progenies of apparent hybrids are composed of two or more types. These facts, however, pertain only to putative hybrids and the conditions favoring hybridization. Although a few garden and artificial hybrids (3,8) have been cited, their characteristics, behavior, and fertility have not been recorded. The present study of artificial hybrids indicates that yuccas are genetically similar and that hybridization among native plants is common.

¹ Agronomist, Crops Research Division, Agriculture Research Service, U.S. D.A., Berkeley, California. Work done in cooperation with Botany Department, University of California, Berkeley, California.

² Numbers in parentheses refer to Literature Cited.

The seeds of the species involved in the hybrids were collected in the following localities:

Yucca glauca Nutt., Grant, New Mexico.

Yucca elata Engelm., White Sands National Monument, New Mexico.

Yucca constricta Buckl., Big Spring, Texas.

Yucca schidigera Roezl ex Ortgies, Riverside, California.

Yucca arizonica McKelv., Nogales, Arizona.

Yucca neomexicana Woot. & Standl., Kenton, Oklahoma.

The pollinations were made at Riverside, California (9), and the hybrids were grown in the University of California Botanic Garden, Berkeley, California. Specimens of the hybrids are in the University of California Herbarium, Berkeley, California.

FERTILITY AND MEIOTIC BEHAVIOR

The percent of F_1 fruit obtained from self-pollinations and the viability of F_1 and F_2 seed are given in Table 1.

The microsporocyte divisions of the hybrids were identical or strikingly similar. Each consistently formed 5 large and 25 small bivalents and exhibited few or no irregularities in either the first or the second division. All tetrads appeared normal, and only 6 percent of the matured grains were abortive.

TABLE 1. PERCENT OF F_1 SELFED FRUIT AND VIABILITY OF F_1 AND F_2 SEED

	Percent germination of F_1 seed*	Percent of F_1 fruit from self-pollinations*	Percent germination of F_2 seed
<i>Y. glauca</i> \times <i>Y. elata</i>	84	88	86
<i>Y. constricta</i> \times <i>Y. schidigera</i>	64	72	72
<i>Y. arizonica</i> \times <i>Y. neomexicana</i>	54	24	68
<i>Y. arizonica</i> \times <i>Y. glauca</i>	62	32	72

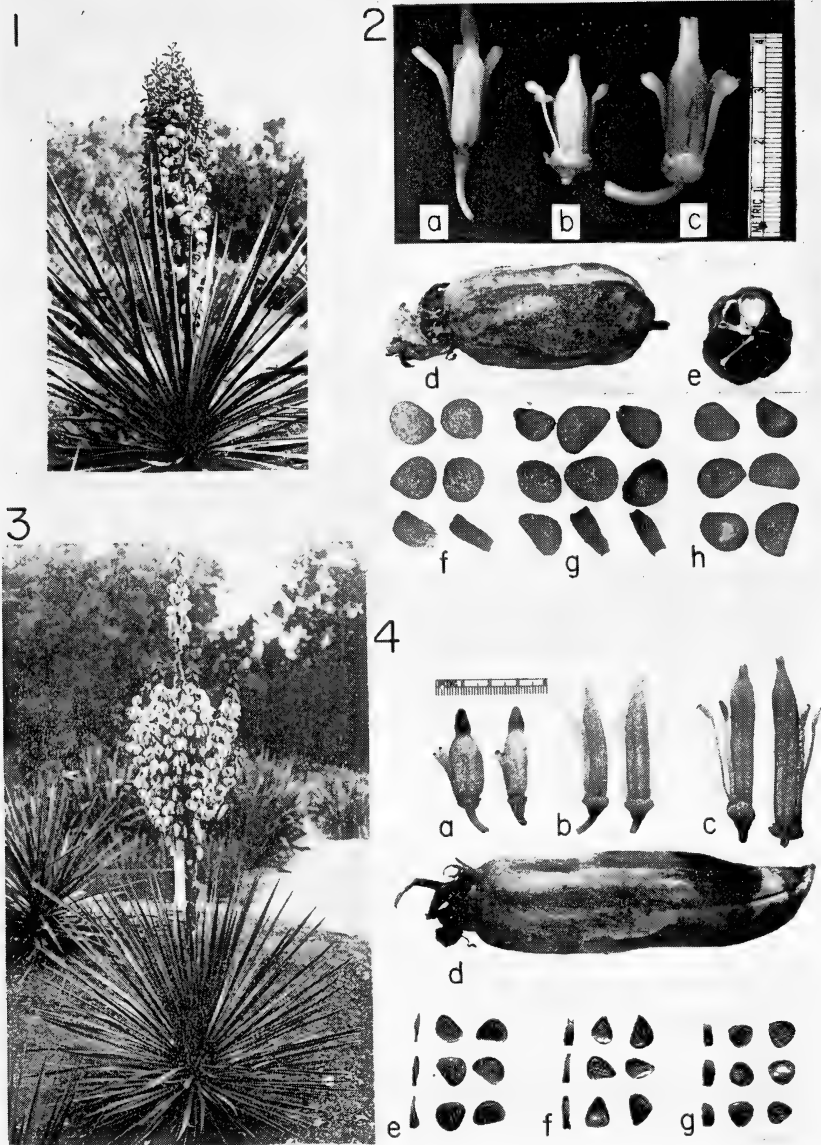
* Fruit percentages based on 25 pollinations and seed germination based on germination test of 50 seeds.

CHARACTERS INDICATIVE OF DERIVATION

The majority of characters of the hybrids are either intermediate in nature or approach those of the parents. The most helpful characteristics in recognizing the derivation of the hybrids are the following:

Yucca glauca \times *Y. elata*: the low height of the inflorescence (7.05 cm. above foliage) and the greenish, swollen styles approximate those of *Y. glauca*, while the large head of leaves and the paniculate inflorescence resemble those of *Y. elata*. The hybrid is very similar to *Y. intermedia* McKelv. var. *ramosa* McKelv. (5,p.120, pl. 46) and to plants reported possibly to be *Y. elata* \times *Y. glauca* hybrids (9, p. 63, pl. 41).

Yucca constricta \times *Y. schidigera* (figs. 1, 2): the non-fleshy fruit (3.20 cm. thick, 6.35 cm. long) and large, angular seeds (7.20 by 11.1 mm.) are characteristic of *Y. constricta*, while the indehiscent fruit and



FIGS. 1-4. *Yucca* parents and hybrids. FIG. 1. Habit of *Yucca constricta* \times *Y. schidigera*. FIG. 2. *Yucca constricta* \times *Y. schidigera* and parents: a, pistil and stamens of *Y. constricta*; b, pistil and stamens of *Y. schidigera*; c, pistil and stamens of hybrid; d, capsule of hybrid; e, cross section of hybrid capsule; f, seeds of *Y. schidigera*; g, seeds of hybrid; h, seeds of *Y. constricta*. FIG. 3. Habit of *Yucca arizonica* \times *Y. neomexicana*. FIG. 4. *Yucca arizonica* \times *Y. glauca* and parents: a, pistil and stamens of *Y. glauca*; b, pistil and stamens of hybrid; c, pistil and stamens of *Y. arizonica*; d, fruit of hybrid; e, seeds of *Y. glauca*; f, seeds of hybrid; g, seeds of *Y. arizonica*.

thick, rough seeds containing ruminate endosperm are characteristic of *Y. schidigera*. The only similar fruits found on native plants (9, p.56, pl.34) occurred on plants belonging to the *Y. glauca* alliance, but these fruits contained typical capsular seeds.

Yucca arizonica \times *Y. neomexicana* (fig. 3) and *Y. arizonica* \times *Y. glauca* (fig. 4) are fairly similar. They differ chiefly in the leaf blades being mainly concavo-convex and the flowers globose in *Y. arizonica* \times *Y. neomexicana*, while the leaf blades are largely plano-convex and the flowers campanulate in *Y. arizonica* \times *Y. glauca*. The most significant features of these hybrids are the following: 1) the non-fleshy, indehiscent fruits and the large, angular, thick, rough seeds containing a ruminate endosperm (fig. 4), which characterize the dehiscent-indehiscent origin of the hybrid; 2) the exceptionally long, conical ovary (3.80 cm.) and fruits (10.3 cm.) (fig. 4), which separate the hybrids from *Y. constricta* \times *Y. schidigera* and possibly characterize all hybrids between species of the *Baccatae* series of McKelv. and dehiscent fruit species; and 3) the paniculate-racemose nature of the inflorescence proper (lower half cuneiform, upper half racemose) (fig. 3), which probably characterizes hybrids between plants with typical paniculate and racemose inflorescences. Although no native plants exhibiting the first two of the preceding features have been reported, those with paniculate-racemose inflorescences are fairly common. Such inflorescences are characteristic of *Y. utahensis* McKelv. and *Y. intermedia*, and they are common among native yuccas reported to be possible hybrids (9, pp.56-68, pl.31, 33, 40).

YUCCA CONSTRICTA \times Y. SCHIDIGERA F_2

Second generation seedlings of only *Y. constricta* \times *Y. schidigera* have been grown. Leaf variations between individuals of a year-old population are as follows: 1.40 cm. wide and 12.0 cm. long to 0.63 cm. wide and 21.3 cm. long; thick, rigid and straight to thin, flexible and falcate; light green to dark green; and thin, entire margin to corneous, denticulate margin. The leaves of several of the seedlings are considerably broader than those of equally as old seedlings of such broadleaved species as *Y. faxoniana* (Trel.) Sarg., *Y. supicola* Scheele, and *Y. gilbertiana* (Trel.) Rydb. Although the seedling leaves of *Y. schidigera* have denticulate margins they become filiferous several months before they are a year old. Corneous, denticulate margins are characteristic of matured leaves in species of the sections of *Hesperoyucca*, *Clistocarpa*, and the series *Rupicola* of McKelv.

DISCUSSION

The normal meiotic behavior and the high fertility of the hybrids indicate that the chromosomes of the parental species are homologous and differ only with respect to certain genes. Furthermore, since the similar karyotypes of yuccas suggest parallel speciation, it is very likely that there is a considerable degree of genetic affinity between the majority of species. Under these conditions it appears that the major barrier to

interbreeding among the native plants of *Yucca* is spatial isolation. Although these suppositions are supported by putative, natural hybrids involving many species, several species are not included. It is very probable, however, that hybrids involving the latter species have not been recognized, or that barriers other than genetic affinity or geographical separation occur.

The fact that no apparent hybrids involving *Y. schottii* Engelm. have been reported is unquestionably due to the late flowering season of this species. Although similar flowering barriers occur between several other species, usually the flowering period within a group of associated species overlaps. The failure of *Y. arizonica* \times *Y. neomexicana* and *Y. arizonica* \times *Y. glauca* to fruit freely was probably due to the long style and closed stigma lobes, which commonly prevented fertilization. It is likely that the capitate stigma of *Y. whipplei* Torr. is a structural barrier and that similar barriers exist in other species.

Although dehiscent- and indehiscent-fruited species are frequently associated, no reputed natural hybrids between them have been reported. In general appearance *Y. constricta* \times *Y. schidigera* resembles an indehiscent, baccate-fruited yucca, while *Y. arizonica* \times *Y. neomexicana* and *Y. arizonica* \times *Y. glauca* resemble a capsular-fruited yucca. If these hybrids were admixed with wild plants, they would undoubtedly be considered hybrids between baccate-fruited species and capsular-fruited species respectively. Their true origin could not be determined without careful examination, unless fruits and seeds were available.

The genera *Yucca* and *Agave* have identical karyotypes (6,10) and a similar distribution (1,8,9), and both are highly unstable (1,7,9). Although much of the diversity in *Agave* is attributed to hybridization, considerable is due to polyploidy, mainly allotetraploidy. The polyploids in *Agave* have a wider distribution and, in general, a greater vegetative development than the diploids (1). No polyploids have been reported in *Yucca*. Both thick, succulent-leaved species (*Y. faxoniana*, *Y. torreyi* Shafer.) and thin, flaccid-leaved species (*Y. constricta*, *Y. glauca*) are diploids (6). Furthermore, the distribution of these diploids is as extensive as the combined diploid-polyploid distribution of *Agave*. *Yucca* extends from south-central Mexico to South Dakota (8,9), whereas *Agave* extends from northern South America to Utah and Nevada (1).

LITERATURE CITED

1. GRAMICK, E. B. 1944. A karyosystematic study of the genus *Agave*. *Am. Jour. Bot.* 31: 283-298, illus.
2. HAINES, L. 1941. Variations in *Yucca Whipplei*. *Madroño* 6: 33-45, illus.
3. MOLON, G. 1914. Monograph, *Le Yucche*. Published in Italian.
4. McKELVEY, S. D. 1938. *Yuccas of the Southwestern United States*. Part One, 150 pp., illus. Jamaica Plain, Mass.
5. ———. 1947. *Yuccas of the Southwestern United States*. Part Two, 192 pp., illus. Jamaica Plain, Mass.
6. ———. and K. SAX. 1933. Taxonomic and cytological relationships of *Yucca* and *Agave*. *Jour. Arnold Arb.* 14: 76-81, illus.

7. STANDLEY, P. C. 1920-1926. Trees and shrubs of Mexico. Contr. U.S. Nat. Herb. 23: 1-1721, illus.
8. TRELEASE, W. 1902. The Yuccae. Missouri Bot. Gard. Ann. Rept. 13: 27-133, illus.
9. WEBBER, J. M. 1953. Yuccas of the Southwest. Agr. Monograph No. 17, U.S. Dept. Agr. 97 pp. illus.
10. WHITAKER, T. W. 1934. Chromosome constitution in certain monocotyledons. Jour. Arnold Arb. 15: 135-143, illus.

REVIEW

The Physiology of Forest Trees, a Symposium held at the Harvard Forest, April, 1958, under the auspices of the Maria Moors Cabot Foundation. Edited by KENNETH V. THIMANN with the assistance of WILLIAM B. CRITCHFIELD and MARTIN H. ZIMMERMAN. xvi + 678 pp., illustr. The Ronald Press. New York, N.Y. \$12.00.

Although principles of plant physiology are the same for all forms of plant life, the methods of research will differ depending on what kind of plants are used in experimental work. Truly, it is a great difference in applying plant physiology to cultivated annuals, such as barley or oats on one hand or to forest trees, that may be several hundred years old and many feet tall, on the other. Plant physiologists, working with forest trees have felt for a long time a need for a get-together to discuss their common problems. Dr. Kenneth V. Thimann, Professor of Biology, Harvard University, was responsible for organizing the first International Symposium on The Physiology of Forest Trees. The symposium was held under the auspices of the Maria Moors Cabot Foundation. Over thirty scholars from several European countries, Canada and United States gathered at the Harvard Forest, Petersham, Massachusetts, in April 1957. The topics discussed included: Water relations and sap movement; Photosynthesis; General Biochemistry; Mineral nutrition; Translocation; Root Growth and other phenomena; Photoperiodism and Thermoperiodism; and Reproduction. The papers were edited by Dr. Thimann, with the assistance of Dr. William B. Critchfield and Dr. Martin H. Zimmermann, and published in one volume. Publication of this volume signifies, if not the birth, at least a formal recognition, of a new branch of Plant Physiology.

The import of this book on the further development of Forest Tree Physiology will be felt for a long time.—N. T. MIROV, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

NOTES AND NEWS

ALPHABETICAL LIST OF FAMILIES FOR MUNZ AND KECK. An alphabetical list of families, giving the page on which each family begins, is available for Munz and Keck, *A California Flora*. It is intended for pasting to the inside of the back cover. Copies may be had by sending a request for the number desired, together with a stamped self-addressed envelope, to Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California.

Some publications of interest follow:

Origin of Primary Extraxylary Stem Fibers in Dicotyledons, by Amélie Blyth. University of California Publications in Botany 30 (2): 145-232, pls. 1-23. 1958. \$1.75.

Secondary Phloem of Calycanthaceae, by Vernon I. Cheadle and Katherine Esau. University of California Publications in Botany 29 (4): 397-510, pls. 60-67, 109 figs. in text. 1958. \$2.25.

*Ontogeny of the Inflorescence and the Flower in *Drimys winteri* var. *chilensis**, by Shirley Cotter Tucker. University of California Publications in Botany 30 (4): 257-336, pls. 24-33, 43 figs. in text. 1959. \$1.50.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers,	
Volumes 1 and 250
Succeeding numbers,	
(except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$6.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany
University of California, Berkeley 4, California



MADRÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 7

JULY, 1960

Contents

	PAGE
SANICULA DESERTICOLA, AN ENDEMIC OF BAJA CALIFORNIA, <i>Peter H. Raven and Mildred E. Mathias</i>	193
A NEW SPECIES OF VALERIANA FROM BRAZIL, <i>Frederick G. Meyer</i>	197
STUDIES IN WESTERN VIOLETS, IX. MISCELLANEOUS SPECIES IN THE SECTIONS NOMIMUM AND CHAMAE-MELANIUM, <i>Milo S. Baker</i>	199
CHROMOSOME NUMBERS IN SILENE (CARYOPHYLLACEAE). II, <i>A. R. Kruckeberg</i>	205
A NEW SPECIES OF ZINNIA FROM MEXICO, <i>A. M. Torres</i>	215
A COMMENT ON COLD SUSCEPTIBILITY OF PONDEROSA AND JEFFREY PINES, <i>Willis W. Wagoner</i>	217
DOCUMENTED CHROMOSOME NUMBERS OF PLANTS	219
REVIEW: Mont E. Lewis, <i>Carex—its Distribution and Importance in Utah</i> (Jack Major)	221
NOTES AND NEWS: EDWARD LEE GREENE CORRESPONDENCE, <i>Robert P. McIntosh</i> ; UROSPERMUM PICROIDES IN BERKELEY, <i>Annetta Carter</i>	222

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$6.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—JOHN H. THOMAS,

Dudley Herbarium, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: Herbert G. Baker, Department of Botany, University of California, Berkeley, California. First Vice-president: Malcolm A. Nobs, Carnegie Institution of Washington, Stanford, California. Second Vice-president: Herbert F. Copeland, Sacramento City College, Sacramento, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: John Thomas, Dudley Herbarium, Stanford University, Stanford, California.

SANICULA DESERTICOLA, AN ENDEMIC OF
BAJA CALIFORNIAPETER H. RAVEN AND MILDRED E. MATHIAS¹

One of the more restricted species of northern Baja California is *Sanicula deserticola* Bell, known from a few disjunct populations at the northern margin of the Sonoran Desert. One population is known from near El Mármol at the headwaters of the Arroyo de San Fernando, while others are in the yellow hills northwest of Rancho Arenoso and near Rancho Aguajito, both in the drainage of the Arroyo del Rosario. At the last-mentioned locality, it was found growing abundantly on the northwest-facing slopes of a yellow conglomerate hill, 3.6 miles west of Rancho Aguajito (Raven, Mathias, and Turner 12,678), associated with *Rosa minutifolia*, *Euphorbia misera*, *Yucca whipplei* *eremica*, *Idria columnaris*, *Eriogonum fasciculatum*, *E. scalare*, *Encelia californica* var. *asperifolia*, *Calandrinia maritima*, *Harfordia macroptera*, *Brodiaea pulchella*, *Layia platyglossa*, and *Filago californica*, as well as two species of *Agave* and one each of *Dudleya*, *Mammillaria*, *Echinocereus*, *Echinocactus*, and *Opuntia*. This curious mixture of characteristic members of the California flora and such species as *Idria columnaris*, restricted to the Sonoran Desert, clearly demonstrates the unique ecological position of *Sanicula deserticola*.

The subfamily Saniculoideae of the Umbelliferae, with some 260 species, like the other subfamilies Hydrocotyloideae and Apioideae, has apparently had a long and independent evolutionary history. The distribution of the extant genera of Saniculoideae shows clearly that they have developed within the Arcto-Tertiary Geoflora and have been associated with it for a long time, perhaps since late Mesozoic time when this Geoflora is first recognized in the fossil record. Several of the genera in this subfamily are restricted to areas of Arcto-Tertiary-derived deciduous forest in eastern Asia. Others range south along mountain chains to Africa. The genus *Eryngium* is world-wide in distribution, whereas the genus *Sanicula* is exceedingly widespread in the Northern Hemisphere, with some of its species occurring also in the Southern Hemisphere. Shan and Constance (1951) considered the section *Sanicula* (*Sanicla*), with about one-third of the species of the genus *Sanicula*, the main trunk of the genus. Some species of this section are widespread in Eurasia, and their present distribution suggests development of the section from a northern stock with subsequent southerly migrations. In North America *S. marilandica* L. and *S. trifoliata* Bickn., which Shan and Constance considered probably the least advanced species, occur as common associates of the eastern deciduous forests. The distribution of this section is therefore closely related to that of the Arcto-Tertiary Geoflora.

¹ The authors would like to acknowledge the helpful suggestions of Dr. Harlan Lewis in the preparation of this paper.

In western North America, the genus *Sanicula* is represented by section *Sanicoria*, which Shan and Constance showed was probably derived from members of section *Sanicula*. *Sanicula deserticola* is one of fourteen species comprising section *Sanicoria*, which is the most diverse within the genus in vegetative and reproductive characters. The development of the Madro-Tertiary Geoflora in early Tertiary time in western North America involved a segregation of species from the dry margins of the tropics and from the Arcto-Tertiary Geoflora,—a segregation fostered by the ever-increasing influence of aridity, particularly the loss of summer rain, and of more extreme temperature variation over much of the West (Axelrod, 1958). Increasing environmental diversity in this area has resulted in large measure from the continuation of this process of progressively increasing aridity, and the evolution of section *Sanicoria* was doubtless correlated with the development of this climatic and topographic diversity. Bell (1954) showed that the different diploid species of section *Sanicoria* differ in their environmental preferences. The existence of localized species in specialized environmental situations is unique to this section. Thus *Sanicula peckiana* F. Macbr. occurs only on serpentine, *S. saxatilis* Greene occurs only on volcanic or serpentinized rocks, *S. arctopoides* H. & A. occupies coastal bluff and dune habitats, and *S. maritima* Kell. is a local species confined to moist adobe soil near the coast. Although some species of the section are less sharply differentiated ecologically, they are, as a class, plants of relatively xeric habitats in chaparral and various oak-conifer woodland associations derived from the Madro-Tertiary Geoflora. One species, *S. graveolens* Poepp., ranges widely north and east, and others occur in suitable sites north along the Pacific Coast, but most of the species of section *Sanicoria* are members of the California flora in the broad sense as delimited by Howell (1957). The occurrence of two mesophytic species of *Sanicula* on the western coast of South America is, we believe, the product of relatively recent long-range transtropical dispersal of the type discussed by Grant (1959) and by Raven and Lewis (1959).

On morphological grounds, the species most closely related to *Sanicula deserticola* is *S. bipinnatifida* Dougl., but nevertheless the two are amply distinct. *Sanicula bipinnatifida* is found colonially in open rocky grassland from Washington south to the northern edge of Baja California, in regions with average annual precipitation ranging from about 12 to 40 inches. The populations of *S. deserticola* are about 150 miles south of the range of *S. bipinnatifida* in a region with an average annual precipitation that ranges from perhaps 2 to 7 inches (fig. 1). It is therefore found in a habitat which with respect to aridity is very extreme for members of section *Sanicoria* and for the genus *Sanicula* as a whole. In its native habitat *S. deserticola* probably flowers whenever it has sufficient water. This is suggested by its flowering response when grown at the University of California, Los Angeles, where it flowered twice a year when supplied with abundant water.

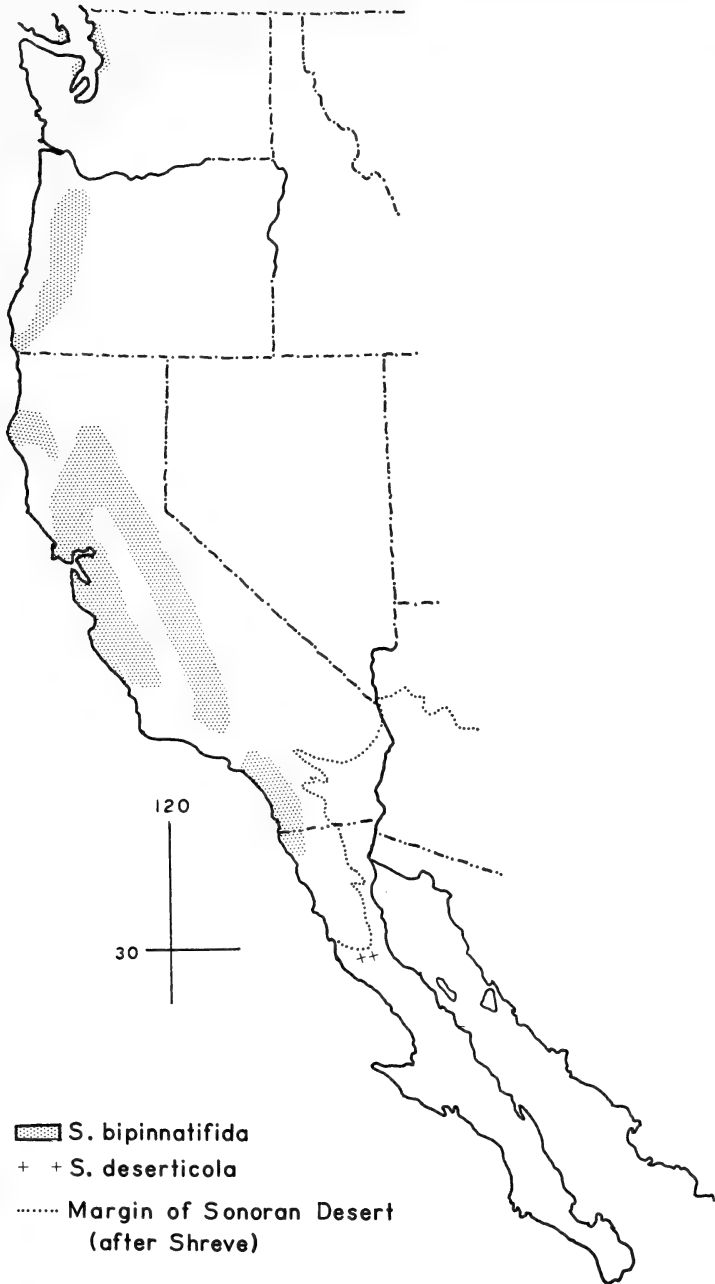


FIG. 1. A portion of western North America, showing ranges of *Sanicula deserticola* and *S. bipinnatifida* and approximate line of demarcation between desert and chaparral in Baja California.

Rodríguez (1957) found that the vessels of *Sanicula deserticola* have the smallest mean length for any member of the family that he examined; this, together with its long taproot and clumped habit, indicate its advanced position compared with *S. bipinnatifida*. One may reasonably infer that populations ancestral to both became differentiated at the southern margins of their distribution in response to an arid climate. The disjunct populations of *S. deserticola* may have been somewhat more continuous during pluvial periods of the Pleistocene, but at which time period this species became spatially and genetically isolated from *S. bipinnatifida* cannot be demonstrated.

The area of *Sanicula deserticola* lies along the southern margins of the transition area between the Californian chaparral and the Sonoran Desert, as defined by Shreve (1936). Shreve noted that species which are endemic in the transition area are preponderantly of northern relationship, while the plants of the desert area are more sharply confined to their own formation. He explained this relationship by the fact that the only requirement for the long southward extension of a chaparral species is a relatively moist habitat, however restricted in area this may be, while the requirements for northward extension of desert species are more complex. The approximate boundary between the two areas is shown in figure 1. *Sanicula deserticola* is certainly such a species of northern affinities. A parallel distributional pattern and relationship are found in the shrubby *Salvia chionocephala* Epling; this species also consists of a few disjunct populations in north-central Baja California, and it is closely related to other species of section *Audibertia*, such as *Salvia leucophylla* Greene. The distribution of most species of *Salvia* sect. *Audibertia* is associated with the California flora and therefore similar to that of *Sanicula* sect. *Sanicoria*.

Within the genus *Sanicula*, the section *Sanicoria*, apparently stemmed from ancestors adapted to relatively mesic sites within the area of the Arcto-Tertiary Geoflora and occupied successively drier and drier habitats offered by the expansion and differentiation of the Madro-Tertiary Geoflora. The species of section *Sanicoria* that occupies the most xeric habitats is *Sanicula deserticola*. Relatively few perennial Umbelliferae occur in such habitats, and most of those that do are members not of Saniculoideae, but of the larger and more diverse subfamily Apioideae.

Department of Botany
University of California
Los Angeles, California

LITERATURE CITED

- AXELROD, D. I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24:433-509.
BELL, C. R. 1954. The *Sanicula crassicaulis* complex (Umbelliferae). Univ. Calif. Publ. Bot. 27:133-230.
GRANT, V. 1959. Natural history of the phlox family. Vol. I. Systematic botany. The Hague: Martinus Nijhoff.
HOWELL, J. T. 1957. The California flora and its province. Leaflet. West. Bot. 8:133-138.

- RAVEN, P. H., and H. LEWIS. 1959. The relationship of clarkias from two continents. *Brittonia* 11:193-205.
- RODRÍGUEZ, R. L. 1957. Systematic anatomical studies on Myrrhidendron and other woody Umbellales. *Univ. Publ. Bot.* 29:145-318.
- SHAN, R. H., and L. CONSTANCE. 1951. The genus *Sanicula* (Umbelliferae) in the Old World and the New. *Univ. Calif. Publ. Bot.* 25:1-78.
- SHREVE, F. 1936. The transition from desert to chaparral in Baja California. *Madroño* 3:257-264.

A NEW SPECIES OF VALERIANA FROM BRAZIL

FREDERICK G. MEYER

Valeriana glechomifolia sp. nov. Herba perennis omnino puberula, longe repens; caulis tenuis foliosus; folia opposita, laminis suborbicularibus vel orbiculari-reniformibus, crenato-dentatis, petiolis 0.6-1.4 cm. longis; inflorescentia erecta, 4-10 cm. longa; flores hermaphroditi; corolla infundibuliformis 2-2.5 mm. longa; achaenia oblonga vel elliptica aliquantulum ampulliformia ubique puberulenta; calycis limbus brevipuliformis plus minusve dentatus.

Uniformly puberulent long-creeping perennial, rooting at the nodes; stems slender, terete, about 1 mm. in diameter, leafy, the internodes 1-2.5 cm. long; leaves opposite, erect or ascending, the blades suborbicular to orbicular-reniform, 0.6-1.5 cm. wide, sometimes truncate at the base, uniformly crenate-dentate, the petioles 0.6-1.4 cm. long; inflorescence an aggregate or compound dichasium, erect, 4-10 cm. long, arising on a slender stalk from leaf axils along the creeping stems, with 1-3 pairs of leaves, the terminal dichotomies about 1-3 cm. wide in anthesis, later more diffuse, the bracts 1-3 mm. long, more or less spathulate, the flowers hermaphroditic; corolla infundibuliform, 2-2.5 mm. long, glabrous, the tube gibbous, the lobes 5, spreading, slightly unequal; stamens 3, exserted, 2-lobed; style 3-lobed; achenes oblong to elliptic, about 1.5 mm. long, somewhat ampulliform, more or less oblique, uniformly puberulent; calyx-limb short-cupuliform, more or less dentate.

Specimens examined. BRAZIL. Santa Catarina, Mun. Bom Retiro: Campo between Fazenda Campo dos Padres and Fazenda Santo Antonio, Campo dos Padres, alt. 1400-1650 m., November 21, 1956, *L. B. Smith & R. Klein* 7800 (type US); same locality, January 24, 1957. *L. B. Smith & R. Reitz* 10383.

The combination of creeping habit and leaves that resemble those of *Glechoma hederacea* quickly distinguishes *V. glechomifolia* from all other New World valerianas. The fruit of *V. glechomifolia* allies it with other Brazilian valerianas with a coronate calyx-limb in the group with *V. salicariifolia*, *V. chamaedryfolia*, *V. foliosa*, and *V. eichleriana*, but the uniformly puberulent and more or less oblique achenes of *V. glechomifolia*



FIG. 1. *Valeriana glechomifolia*: A, habit, $\times \frac{3}{4}$; B, inflorescence and single leaf, $\times 3$; C, fruit, flower, and stamens, $\times 10$, Smith & Klein 7800.

differ from the uniformly glabrous and regular achenes of the aforementioned Brazilian species.

Students of South American *Valeriana* reserved the segregate genus *Phyllactis* for species with coronate calyx. My own studies previously on North American species and now on those of South America indicate that single character differences, especially floral differences, are insufficient in differentiating segregate genera. Indeed, the specialized calyx, either coronate or pappus-like, and more especially the sculpturing of the cypselate achene combine with vegetative characters in the differentiation of species of South American *Valeriana*.

This interesting discovery by Lyman B. Smith of the Smithsonian Insti-

tution, Washington, D.C., is one of a long series of new plants discovered on Dr. Smith's fruitful collecting trip to Santa Catarina in 1956-57.

Crops Research Division, Agricultural Research Service
U.S. Department of Agriculture
Beltsville, Maryland

STUDIES IN WESTERN VIOLETS, IX.
MISCELLANEOUS SPECIES IN THE SECTIONS *NOMIMUM*
AND *CHAMAEMELANIUM*

MILO S. BAKER

This paper treats four taxa of *Viola* in the sections *Nomimum* and *Chamaemelianum*—a newly described species, a change of status from species to subspecies for a second taxon, observations confirming the specific status of a third taxon, and a newly described subspecies. In addition to my own specimens at the North Coast Herbarium, I have cited specimens from the United States National Herbarium, the New York Botanical Garden, the California Academy of Sciences, and the University of California Herbarium; to the curators of these latter herbaria I express my appreciation.

***Viola Aliceae* sp. nov.** Herba exigua omnino puberulenta cauli supraterrano brevissimo suppressoque et rosella basali foliorum ac floribus uno duobusque folias parum excedentibus instructa cauli subterraneo gracili bracteas squamas simulantes gerente, tota ex radice fusiformi longitudine variabili (ut apud specimina typica videtur) crescens; folia oblongo-ovata vel elliptica obscure undulato-dentata decurrentia 2 vel 3 cm. longa dimidio lata petiolis laminas longitudine aequantibus; stipulae inconspicuae lanceolatae marginis laceratis; flores caesii longitudine 1 cm. parum excedentes petalis angustis eis lateralibus aliquantulo barbatis; stigma ut id *Violae aduncae* ebarbatum; et capsula et semina hucusque ignoti.

A small plant, 5 to 11 cm. high, caulescent but the aerial stem undeveloped, bearing a rosette of leaves and one or two flowers slightly above the leaves; finely puberulent throughout; subterranean stem slender with scale-like bracts; taproot variable in length (as in type sheet); leaves long-ovate to elliptic, obscurely undulate-dentate, decurrent, 2 to 3 cm. long and half as wide, on petioles about as long; stipules inconspicuous, lanceolate with lacerate margins; flowers lavender, slightly more than 1 cm. long; petals narrow, the lateral slightly bearded; stigma like that of *Viola adunca* but without beards; capsule and seeds unknown. Figs. 1, 2.

Type. MEXICO. Near kilometer 34 post on Mexico City-Cuernavaca highway, altitude 9000 feet, *A. Y.* and *J. E. Wilcox* in 1948 (UC 1,200,-778). Topotype. *A. Y.* and *J. E. Wilcox* 22, 1946. *Viola Aliceae* should be

assigned to Section *Nomimum* Ging., although the stigma and style are somewhat different from other members of this section.

When making their second collection of the violet in 1948, the one cited above as the type, Mr. and Mrs. Wilcox dug deeply to investigate the character of the root system. In 1952 they returned to the type locality, but a diligent search of several hours failed to reveal any plants of this violet.

In some cases the underground stem measures only a few centimeters, and could represent the normal growth from a seed over a few years, such as the upper right hand plant (topotype, *Wilcox 22*) on the type sheet. In other cases the vertical subterranean stem is very slender and possesses a number of scale-like bracts at more-or-less regular distances apart, such as the plant on the upper-left-hand side of the type sheet (type collection, *Wilcox* in 1948). How such a stem was formed is not clear. It might be formed by underground stolons from another plant such as that represented by the topotype. However, I do not know of such a case in any other species of *Viola*.

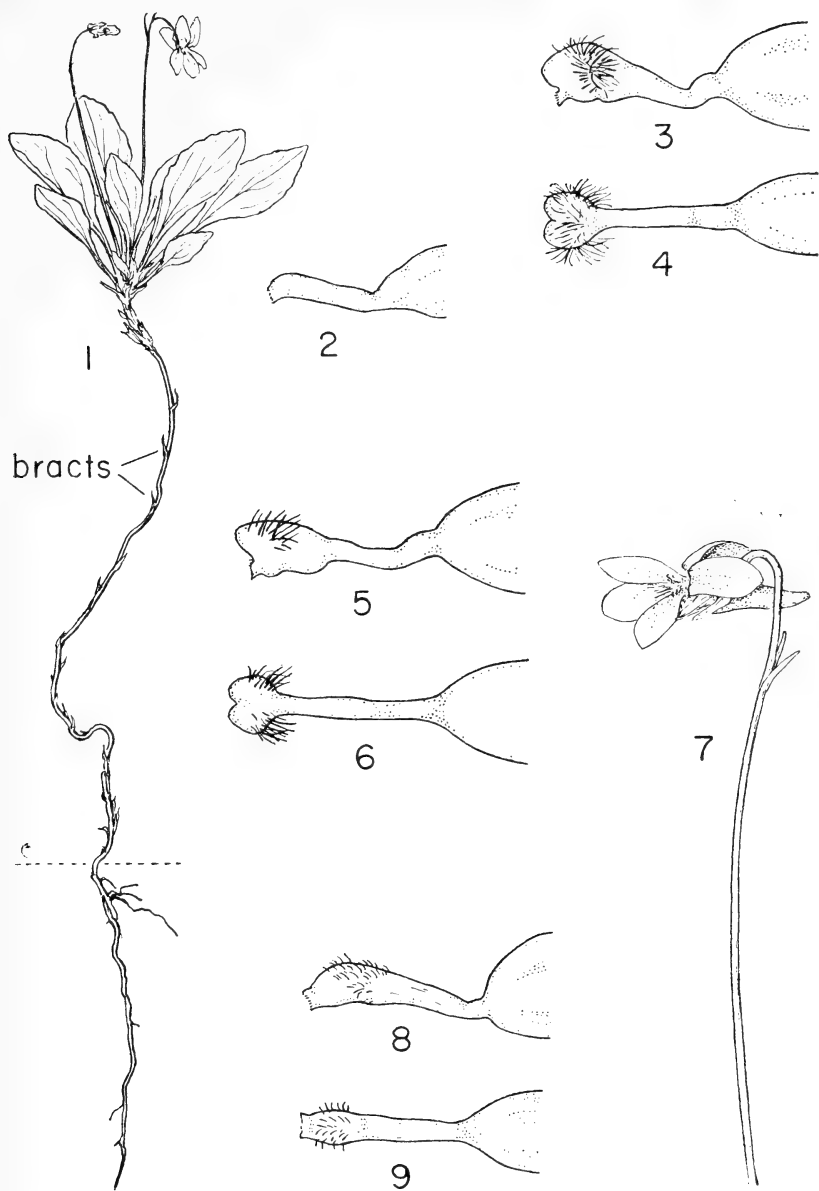
Two other collections of *Viola* resemble *V. Aliceae* in having similar slender underground stems as well as similar style and stigma, but they differ from that species in being wholly glabrous [*Quebrada Honda*, *Durango*, *Palmer 227* (US, NY); *Sierra Madre near Chihuahua*, *Townsend & Barber 94* (US, NY)]. Their exact relationship to *V. Aliceae* cannot be determined at this time. Some of the plants on the *Palmer* sheet, however, represent another species unrelated to *V. Aliceae*.

VIOLA LOBATA Benth. subsp. **psychodes** stat. nov. *V. psychodes* Greene, *Pittonia* 3:318. 1898.

In 1898, E. L. Greene proposed the name *V. psychodes* for a violet collected near Waldo, Oregon. Since then, this taxon has been collected at many locations in California. In general *V. psychodes* resembles *V. lobata*, which is abundant in California. The differences between these two taxa do not seem of sufficient magnitude to merit retention of both of them as species; therefore I propose treating *V. psychodes* as a subspecies of the common *V. lobata* Benth, section *Chamaemelum* Ging. Both have similar root systems, a naked stem with leaves and flowers borne near the summit, leaves that may be variously lobed or even entire, and similar pistils (figs. 3–6). Plants of both taxa have the habit of producing a single radical leaf for the first year.

There are, however, some differences between the two, the most significant being that subsp. *psychodes* is glaucous throughout, while *V. lobata* is puberulent. Another difference is leaf thickness—the average for *V. lobata* is 0.0036 inch, while for subsp. *psychodes* it is 0.0057 inch. The measurements for these averages were obtained from leaves of ten collections of each taxon, using a Starrett micrometer which is accurate to one ten thousandths of an inch.

It may be of interest to note that several of the collections of subsp.



FIGS. 1-9. *Viola*. FIGS. 1, 2, *V. Aliceae*: 1, habit, $\times \frac{3}{4}$; 2, pistil, side view. FIGS. 3, 4, *V. lobata* subsp. *lobata*: 3, pistil, side view; 4, pistil, dorsal view. FIGS. 5, 6, *V. lobata* subsp. *psychodes*: 5, pistil, side view; 6, pistil, dorsal view. FIGS. 7, 8, 9, *V. oxyceras*: 7, flower, $\times 1\frac{1}{2}$; 8, pistil, side view; 9, pistil, dorsal view. All pistil illustrations $\times 9$.

psychodes were made in serpentine areas, but I have not been able to ascertain whether or not the plant is restricted to serpentine soil.

Representative specimens. OREGON. JOSEPHINE COUNTY: Little Rock Creek, 2 miles southwest of O'Brien, *Constance & Rollins 2995* (NCH, UC); open woods near Waldo, Oregon, April 20, 1887, *Howell* (UC); near Kirby, *Baker 5526* (NCH). CALIFORNIA. Hearst Castle [Sacramento Canyon], July 22, 1902, *Setchell & Dobie* (UC); serpentine on west side of Sacramento River Canyon, *Wagnon 1616* (NCH). BUTTE COUNTY: east of Oroville, west of Brush Creek Ranger Station, *Cantelow 4527* (CAS). DEL NORTE COUNTY: on serpentine, Gasquet, *Baker 211* (NCH), *Baker 285* (NCH); near Gasquet, *Tracy 10011* (UC); headwaters Shelly Creek, Oregon Mountain, *Hoffman* (NCH). PLUMAS COUNTY: Highway 39 east of summit near Mineral, *Baker 8104* (NCH). SHASTA COUNTY: Delta, *Applegate 5396* (NCH); Castella, June 19, 1923, *Bethel* (CAS); Castle Rock, *Ripley & Barneby 9642* (CAS); on serpentine, Dunsmuir, *Baker 8050* (CAS, UC), *Hall & Babcock 4031* (UC), *Heller 7927* (UC); on serpentine, Shasta Retreat, July 4, 1911, *Condit* (UC); Mount Eddy (some genes of *V. lobata* Benth.), June 1, 1946, *Parker* (UC). SISKIYOU COUNTY: Rainbow Ridge above Sulloway Creek, about 1½ miles west of Mount Shasta City, June 13, 1936, *Babcock & Stebbins 2000* (UC); near Mount Shasta City, *Baker 5525* (NCH); serpentine on east slope Scott Mountain, *Hoffman 2434* (NCH); 6½ miles north of West Brand Road, Happy Camp, *Hoffman 2572* (NCH); trail 1 mile west of Lookout, Clear Creek, *Hoffman 3514* (NCH). TRINITY COUNTY: near Granite Peak, *Baker 205* (NCH); Minersville to Trinity Center, *Eastwood & Howell 4912* (CAS); between Baylers and Trinity Center, *Hoffman 2420* (NCH); Trinity Alps Resort, *Cantelow 995* (CAS); North Fork Mountain, 3500 feet, *Hoffman 3504* (NCH); near boundary of Trinity and Siskiyou counties, Scott Mountain, *Howell 13618* (CAS); north slope of Scott Mountain, 3700 feet, *Cantelow 1453* (CAS); south slope of Scott Mountain, *Cantelow 1452* (CAS); Scott Mountain Road, 11½ miles north of Carrville, June 9, 1939, *Cantelow* (CAS); Nash Mine near Carrville, June 23, 1931, *Van Dyke* (CAS); 17 miles north of Carrville, May 21, 1936, *Cantelow* (CAS); 3 miles north of Carrville, May 21, 1936, *Cantelow* (CAS).

VIOLA OXYCERAS Greene. On the Pacific Coast of North America there are two distinct species of caulescent blue-flowered violets in the section *Nomimium* Ging.: *V. adunca* J. E. Smith, which is found from sea level to a fairly high altitude, and *V. oxyceras* Greene, which grows in the mountains down to about 4000 feet. The latter was considered by Sereno Watson to be only a variety of what we now call *V. adunca* [*V. canina* var. *oxyceras* Wats., Brew. and Wats., Bot. Calif. 1:56. 1876]. This viewpoint may have arisen because in some localities interbreeding between these two species has produced intermediate forms; at most localities, however, the pure types remain distinct.

Aside from their similarity in flower color, the two have little in common. The leaves of *V. adunca* are ovate, more or less subcordate at the base, and have a pointed apex; those of *V. oxyceras* are much thinner, sometimes wider than long, with a cuneate or truncate base (never cordate), and are rounded at the apex. The foliage of *V. adunca* shows some puberulence (except for occasional glabrous races), while that of *V. oxyceras* is without exception entirely glabrous. The form of the flower in these two is different; the flowers of *V. adunca* are larger, having the petals spread in approximately one plane, and having a rather blunt spur; those of *V. oxyceras* are smaller, the upper four petals lie mostly in one

plane, but the lower petal lies below in another plane (fig. 7). The beak of the style in *V. adunca*, although always directed essentially downward, may be pointed forward, or may be at right angles to the axis of the style, or may even assume a still more reflexed position, and it has always a smaller diameter than the head of the style. The beak of *V. oxyceras*, with its stigmatic tube always pointing forward, is very different, having a diameter nearly as large as the head of the style (figs. 8, 9).

The seeds of *V. adunca* and *V. oxyceras* differ also, in both shape and in size. Although the seeds of *V. adunca* vary quite widely in size, they are never as small as the seeds of *V. oxyceras*. But more important than size, the seeds of these two taxa are of different shape. The more rounded seed of *V. oxyceras* is indicated by a length to width ratio of 1.85 to 1, while in the case of *V. adunca* (from six localities) the ratio is 1.98 to 1. With these differences in mind, the maintenance of the two species seems justified.

Representative specimens. CALIFORNIA. High mountain near Donner Pass, 1865, *Torrey 34* (UC), type of *V. canina* var. *oxyceras* Wats. ALPINE COUNTY: Lake Alpine, *Allen 542* (UC); near Lake Alpine, 7,500 feet, *Peirson 11567* (UC). AMADOR COUNTY: Silver Lake, 7,500 feet, *Baker 8557* (NCH). BUTTE COUNTY: Jonesville, 1,500 m., *Copeland 662* (UC); Jonesville, *Copeland 1219* (NCH). EL DORADO COUNTY: Highway 50, 1 mile east of Strawberry, 6,500 feet, *Robbins 1712* (UC); near Lyons Creek about 4 miles south of Wright Lake, 6,700 feet, *Robbins 2020* (CAS, UC), *Robbins 2022* (NCH). FRESNO COUNTY: Vidette Creek, 10,500 feet, 1948, *Dyer* (CAS); Bubb's Creek, at base of East Vidette, 1948, *Chabaud* (CAS); Second Recess, 9,000 feet, *Raven 5697* (CAS). INYO COUNTY: Cottonwood Lakes, 11,000 feet, *Alexander & Kellogg 3417* (UC). TULARE COUNTY: Tyndall Creek, 1916, *Campbell* (CAS). LASSEN COUNTY: Summit Lake, *McCalla 646* (NCH); east fork of King Creek on Cinder Cone Trail, 7,000 feet, *Jepson 4110* (JEPS). MARIPOSA COUNTY: Eagle Peak, Yosemite, 7,200 feet, *Jepson 4372* (JEPS). MODOC COUNTY: High Grade District, northern Warner Mountains, 7,000 feet, *Smith 948* (JEPS). PLACER COUNTY: above Donner Lake, *Copeland 1883* (UC); below Cisco, *Heller 12713* (UC); Summit Valley, *Howell 18577* (CAS). PLUMAS COUNTY: Little Grass Valley, *Baker 9966* (NCH); 1½ miles west of Johnsville, 5,300 feet, *Cantelow 4560* (CAS). SHASTA COUNTY: 22 miles southeast of McCloud, *Cantelow* (NCH). SIERRA COUNTY: Webber Lake, 8,000 feet, *Baker* (NCH). SISKIYOU COUNTY: Marble Mountain, *Chandler 1585* (NCH). TEHAMA COUNTY: near Morgan, 5,500 feet, *Hall & Babcock 4326* (UC). TULARE COUNTY: Camp 170, nine miles north of Mt. Silliman, *Brewer 2807* (UC); South Fork Kaweah River, 8,500 feet, *Ferris & Lorraine 10850* (UC); Center Basin, 11,200 feet, 1948, *Howell 25057* (CAS); Second Lake, Center Basin, 11,400 feet, *Munz 12565* (NCH). TUOLUMNE COUNTY: Kennedy Lake, *Hoover 1458* (UC).

VIOLA BAKERI Greene subsp. *shastensis* subsp. nov. A subspecies *Bakeri* capsulis pubescentibus et paginis sepalorum pilos paucos breves adpressos gerentibus discedit.

This subspecies differs from *V. Bakeri* subsp. *Bakeri* (section *Chamaemelanium* Ging.) in its pubescent capsules and in the presence of a few short appressed hairs on the faces of the sepals.

During the flowering stage, before the appearance of the capsules, subsp. *shastensis* may be distinguished from subsp. *Bakeri* by a careful examination of the sepals. In subsp. *Bakeri*, the faces of the sepals are

entirely glabrous and without any short, appressed hairs such as those found on the faces of the sepals in subsp. *shastensis*. In other respects, as far as I have observed, these taxa are identical.

Type. Postpile Camp, altitude 6000 feet, western Tehama County, California, July 1, 1955, *Baker 13045* (UC 1,199,915); topotype, July 10, 1954, *Baker 12961* (NCH).

Since its discovery in western Tehama County in 1954, *V. Bakeri* subsp. *shastensis* has been found to occur from southern Oregon south in the western slopes of the Sierra Nevada of California to Amador County, as detailed below.

Other collections. OREGON: Road to Dutchman's Peak, May 30, 1938, *Rowntree* (NCH). CALIFORNIA. TRINITY COUNTY: Scott Mountain, *Cantelow 4576* (CAS), *Baker 13139* (NCH), *Wagnon & Barbe* (NCH). LASSEN COUNTY: "devastated area" earth slide, Highway 89, north side Mount Lassen, *Baker 11975* (NCH). AMADOR COUNTY: Silver Lake, altitude 7,400 feet, *Wagnon 1620* (NCH).

One may ask, why should such inconspicuous characters justify the creation of a new subspecies? Our reply is that in the subsection *Nuttallianae* Becker, naked capsules have long been regarded as a diagnostic character separating the *V. Nuttallii* species complex from the *V. purpurea* complex. However, recent studies in *V. praemorsa* of the *Nuttallii* complex have shown that two subspecies have some puberulence of the capsules. Nevertheless, the most widely distributed subspecies, *V. praemorsa* subsp. *major* (Hook.) Baker, subsp. *linguaeifolia* (Nutt.) Baker, and subsp. *praemorsa* have naked capsules.

One also wonders how and when subsp. *shastensis* derived its characters. Examination of *V. praemorsa* subsp. *arida* Baker and subsp. *oregona* Baker & Clausen reveals the fact that they both possess the same pattern of sepal pubescence as does *V. Bakeri* subsp. *shastensis*. In addition, these two subspecies of *V. praemorsa* have more or less pubescence on their capsules. Although there is no known overlap at the present time in the distribution of *V. Bakeri* subsp. *shastensis* and these two Great Basin subspecies of *V. praemorsa*, it is known that an arm of the Great Basin Flora extends from southern Oregon southwest along the Klamath River into the Shasta and Scott valleys, and this lends credence to the belief that *V. praemorsa* subsp. *arida* will be found to occur somewhere in this area not far distant from where we collected *V. Bakeri* subsp. *shastensis*.

From bud fixations of subsp. *shastensis* made in the Scott Mountains, (*Baker 13133, 13139*) Dr. Jens Clausen and Dr. Malcolm Nobs of the Carnegie Institution of Washington at Stanford obtained a chromosome count of $2n = 48$, showing this taxon to be an octoploid. *Viola Bakeri* subsp. *Bakeri* and *V. praemorsa* subsp. *arida* and subsp. *oregona* are also octoploid, $2n = 48$. Therefore, it may be assumed that gene interchange could have taken place between these entities at some past time, thus possibly accounting for the pubescence of the sepals and capsules of *V. Bakeri* subsp. *shastensis*.

Santa Rosa Junior College
Santa Rosa, California

CHROMOSOME NUMBERS IN SILENE (CARYOPHYLLACEAE). II.

A. R. KRUCKEBERG¹

The accumulation of cytotaxonomic data from members of the subfamily Silenoideae (Caryophyllaceae) continues, with this second report adding chromosome numbers of thirty-two species counted for the first time. Additional records are given here for twenty of the species included in the first paper of this series (Kruckeberg, 1954). In all, the present report comprises chromosome counts for one hundred and fifty-six collections from continental North America, Hawaii, Europe, and Asia. The chromosome numbers are listed in Table 1; figures 1–28 are camera lucida drawings of chromosome complements for species hitherto uncounted.

Records of chromosome numbers of the Silenoideae are being accumulated for two reasons. Chromosome counts have intrinsic value as part of the total self-portrait of a taxon. Secondly, the ploidy level of any two populations qualifies the success with which those population samples can be used in hybridizations to determine species interfertilities (see Kruckeberg, 1955).

All counts have been made from squashes of microsporocytes handled in the manner outlined in Kruckeberg (1954). Most of the material I have collected in native habitats of western United States. Collections from eastern United States and from localities outside continental North America were kindly furnished by other botanists.

TABLE 1. DIPLOID CHROMOSOME NUMBERS IN LYCHNIS AND SILENE

WESTERN NORTH AMERICAN SPECIES	2n Chromosome Number	Number of Collections
<i>Lychnis drummondii</i> (Hook.) Wats.	48	5
<i>Silene aperta</i> Greene	48	1
<i>S. bridgesii</i> Rohrb.	48	1
<i>S. californica</i> Durand. Tetraploid	48	2
Hexaploid	72	1
<i>S. campanulata</i> Wats.	48	1
<i>S. clokeyi</i> H. & M.	96	1
<i>S. douglasii</i> Hook.	48	22
<i>S. grayi</i> Wats.	48	3
<i>S. hookeri</i> Nutt. ex T. & G.	72	3
<i>S. invisa</i> H. & M.	48	3
<i>S. laciniata</i> Cav. subsp. <i>major</i> H. & M. Octoploid	96	4
<i>S. laciniata</i> Cav. subsp. <i>greggii</i> (Gray) H. & M. Tetraploid	48	10
<i>S. lemmonii</i> Wats.	48	5

¹ Supported by funds from the State of Washington Initiative No. 171 and by the National Science Foundation, Grant G-1323.

	2n Chromosome Number	Number of Collections
<i>S. marmorensis</i> Kruck.	48	1
<i>S. menziesii</i> Hook. Diploid	24	2
Tetraploid	48	12
<i>S. montana</i> Wats.	48	4
<i>S. nuda</i> (Wats.) H. & M.	48	3
<i>S. nuda</i> subsp. <i>insectivora</i> (Hend.) H. & M.	48	1
<i>S. occidentalis</i> Wats.	48	1
<i>S. oregana</i> Wats.	48	1
<i>S. parishii</i> Wats.	48	3
<i>S. parryi</i> (Wats.) H. & M. Tetraploid	48	9
Octoploid	96	6
<i>S. petersonii</i> Maguire	96	2
<i>S. repens</i> Patrin subsp. <i>australe</i> H. & M.	24	2
<i>S. sargentii</i> Wats.	48	3
<i>S. scaposa</i> Robins.	48	1
<i>S. scouleri</i> Hook.	48	1
<i>S. spaldingii</i> Wats.	48	1
<i>S. thurberi</i> Wats.	48	1
<i>S. verecunda</i> Wats. subsp. <i>verecunda</i>	48	1
<i>S. verecunda</i> Wats. subsp. <i>andersonii</i> (Clokey) H. & M.	48	1
<i>S. verecunda</i> Wats. subsp. <i>platyota</i> (Wats.) H. & M.	48	10
<i>S. williamsii</i> Britt.	24	2
<i>S. wrightii</i> Gray	96	1
EASTERN NORTH AMERICAN SPECIES		
<i>Silene antirrhina</i> L.	24	1
<i>S. caroliniana</i> Walt.	48	2
<i>S. caroliniana</i> subsp. <i>wherryi</i> (Small) Clausen	48	1
<i>S. polypetala</i> (Walt.) Fern. & Schub.	48	1
<i>S. regia</i> Sims.	48	2
<i>S. rotundifolia</i> Nutt.	48	1
<i>S. stellata</i> (L.) Ait. <i>sensu lat.</i>	48	5
<i>S. subciliata</i> Robins.	48	1
<i>S. virginica</i> L.	48	1
SPECIES OUTSIDE CONTINENTAL NORTH AMERICA		
<i>Lychnis wilfordii</i> Maxim.	24	1
<i>Petrocoptis pyrenaica</i> Braun.	24	1
<i>Silene keiskei</i> Miq.	24	2
<i>S. repens</i> Patrin. var. <i>latifolia</i> Turcz.	48	2
<i>S. struthioloides</i> Gray	24	1
<i>S. species</i> from Nepal	24	2

DISCUSSION

Having determined chromosome numbers for all but five of the thirty-three perennial species of *Silene* native to western North America, I am emboldened to make some guarded generalizations. Though chromosome numbers of the remaining uncounted species as well as any additional records for species previously counted may prove to be further exceptions, it seems safe to state that the tetraploid level ($2n=48$) is by far the common one among the western species. The tetraploid level is main-

tained even more rigidly for the eastern North American species. Apart from *S. ovata* and *S. nivea* (Nutt.) Otth., for which chromosome numbers are not yet known, the other seven eastern perennial species are uniformly tetraploid. The present data emphasize the observation made in an earlier paper (Kruckeberg, 1954)—namely, that North America is the home of the polyploids whereas the continental areas of Eurasia are inhabited predominantly by diploid species. At first glance, this geographic difference in average ploidy level might suggest that the Eurasian species were ancestral to the North American ones. The Siberia-Aleutian Islands land bridge, a path well beaten by the biogeographers—if not by the biota themselves—would seem the likely route. Yet one species for which I have obtained counts on both the Asian and North American plants defies the usual west-to-east migration route. *Silene repens* Patrin in Japan (var. *latifolia* Turcz.) is tetraploid while the North American variety, *australe* Hitch. & Maguire, is diploid. Therefore, I would offer an alternative hypothesis: North American polyploid species could have originated on this continent from diploids as a common phenomenon whereas polyploidy might have been a rare event among the ancestors of the Eurasian *Silenes*.

The present list of chromosome numbers permits tentative conclusions to be drawn about certain species.

1. *SILENE CALIFORNICA* DUR. AND *S. HOOKERI* NUTT. On morphological grounds it is easy to see a close relationship between *S. californica* and *S. hookeri*. The prostrate habit, the showy flowers (red versus pink), the characteristic geniculation of the pedicels in fruit, the large black seeds, and the partial sympatric distribution in the Coast Ranges and Siskiyou Mountains all suggest a close affinity. Up to now, though, I was convinced that the two species were isolated by a barrier of ploidy difference. *S. hookeri* is consistently hexaploid ($2n=72$) while most collections of *S. californica* have been tetraploid ($2n=48$). The discovery of a hexaploid *S. californica* population and the subsequent production of a fertile F_1 hybrid (to be discussed in a later paper) support my intuitive feeling that the two species are closely related.

2. *THE THREE SUBSPECIES OF SILENE LACINIATA* CAV. According to Hitchcock and Maguire (1943), three regional facies of *S. laciniata* occur in the southwest. *Silene laciniata* subsp. *laciniata* is widespread in Mexico, *S. laciniata* subsp. *major* H. & M. is confined to coastal southern California, and *S. laciniata* subsp. *greggii* (Gray) H. & M. occurs in Arizona, New Mexico, Texas, and adjacent northern Mexico. Subspecies *major* is octoploid ($2n=96$) while subsp. *greggii* is tetraploid ($2n=48$). Much wider sampling of this polymorphic species will be necessary before it can be fully evaluated cytotaxonomically. Since subsp. *major* and subsp. *greggii* are isolated both spatially and genetically, it becomes a moot question as to whether subsp. *greggii* should be restored to its former level of

species. The center of distribution of *S. laciniata* is undoubtedly in the plateau and mountain regions of north-central Mexico. Subspecies *greggii* is a mid-continent derivative from this center while subsp. *major* is the coastal segregate. Additional collections of *S. laciniata greggii*, made in Arizona, New Mexico, and Texas in the summer of 1959, proved also to be tetraploid. However, in the two weeks of searching in the Mexican states of Nuevo León and Chihuahua, I did not encounter any plants of *S. laciniata*, though the species is frequently reported from this section of México.

3. DIPLOID AND TETRAPLOID *SILENE MENZIESII* HOOK. Further sampling of this wide-ranging species reaffirms my earlier report (Kruckeberg, 1954) of the predominance of the tetraploid level ($2n=48$). As against twelve collections of tetraploids, only two diploid samples are recorded in this current listing. One of the diploids was collected in the Sierra Nevada of California and the other in central Idaho. It would appear that the distribution of diploids is random and their occurrence rare. It is possible that the tetraploids are autopolyploid in origin. The sporadic distribution of the diploids, plus the not infrequent occurrence of quadrivalent pairing in certain tetraploids lends support to this hypothesis. Amphiploid origin is less likely, even though the Idaho diploids do occur sympatrically with another diploid species, *S. repens* Patrin subsp. *australis* H. & M. Apart from being rhizomatous and having general vegetative similarity, North American *S. repens* is not too likely a parent for tetraploid *S. menziesii*.

4. TETRAPLOID AND OCTOPLOID *SILENE PARRYI* (WATS.) H. & M. With the present data it is now possible to define rather clearly the limits of the two ploidy levels in *S. parryi*. The tetraploid forms ($2n=48$) occur exclusively east of the crest of the Cascade Range, and then eastward to the mountains of northeastern Washington (and presumably northern Idaho), terminating in the Rocky Mountains of Montana and Canada². The octoploid segment ($2n=96$) of the species has a much more restricted distribution; as yet it has been found only along the Cascade Range and the Olympic Mountains of Washington.

² A collection of a tetraploid *parryi* made on Snowdrift Mountain in southern Idaho (Kruckeberg 4520) suggests that the tetraploid form extends southward along the Continental Divide.

EXPLANATION OF FIGURES 1-12

FIGS. 1-12. Chromosomes of *Silene* microsporocytes. FIG. 1. *S. aperta*, II M (Kruckeberg 3407). FIG. 2. *S. clokeyi*, Diak. (Kruckeberg 3911). FIG. 3. *S. grayi*, Diak. (Kruckeberg 3772). FIG. 4. *S. invisa*, I M (Kruckeberg 2897b). FIG. 5. *S. laciniata greggii*, Diak. (Kruckeberg 3878). FIG. 6. *S. lemmonii*, Diak. (Kruckeberg 3530). FIG. 7. *S. montana*, Diak. (Kruckeberg 3529). FIG. 8. *S. occidentalis*, I T (Kruckeberg 3696). FIG. 9. *S. petersonii*, Diak. (Kruckeberg 3904). FIG. 10. *S. repens australis*, Diak. (Kruckeberg 4290). FIG. 11. *S. scaposa*, Diak. (Kruckeberg 4031). FIG. 12. *S. spaldingii*, Diak. (Daubenmire, s.n.). Diak., diakinesis; I M, first metaphase; II M, second metaphase; I T, first telophase. →



FIGS. 1-12. Chromosomes of *Silene* microsporocytes.

5. *SILENE WILLIAMSII* BRITT., *S. SEELEYI* MORT. & THOMPS., AND *S. MENZIESII* HOOK. These three species are grouped together because of their close morphological kinship. *Silene williamsii* of central Alaska and *S. seeleyi* are both diploid so far as is known. The fact that some collections of *S. menziesii* are also diploid makes gene exchange among the three species potentially possible. Hitchcock and Maguire (1947, p. 48) speculate that exceptional specimens of *S. menziesii* from western Canada show "contamination" with *S. williamsii*. I have made artificial hybrids in various combinations with the three diploids; some of the hybrids are reasonably fertile. Details of these and other interspecific hybridizations will be discussed elsewhere.

GEOGRAPHIC DISTRIBUTION OF COLLECTIONS

The origin of each collection that provided a chromosome count is given below. All collections are represented by specimens deposited in the University of Washington Herbarium. To those botanists who collected living plant material for this study, the author wishes to express his sincere appreciation.

WESTERN NORTH AMERICAN SPECIES

LYCHNIS DRUMMONDII (Hook.) Wats. $2n=48$. ARIZONA. Apache County: 12 miles from Red Rock, Lukachukai Mountains, *Gould and Phillips 4835*. Coconino County: Head of Kaibab Trail, north rim of Grand Canyon, *Kruckeberg 3901*. NEVADA. Clark County: ridge along trail to Charleston Peak, *Kruckeberg 3910*. NEW MEXICO. Catron County: between Bursom Forest Camp and Willow Creek, Mogollon Mountains, *Kruckeberg 4658*; 5 miles northeast of Collins Park on road to the plains of St. Augustine, *Kruckeberg 4702*.

SILENE APERTA Greene. $2n=48$. CALIFORNIA. Tulare County: 1 mile west of Hockett Meadows, on trail to Atwell Mill, Sequoia National Park, *Kruckeberg 3407*.

SILENE BRIDGESII Rohrb. $2n=48$. CALIFORNIA. Tuolumne County: Hog Ranch, near Mather, *Pray s.n.*

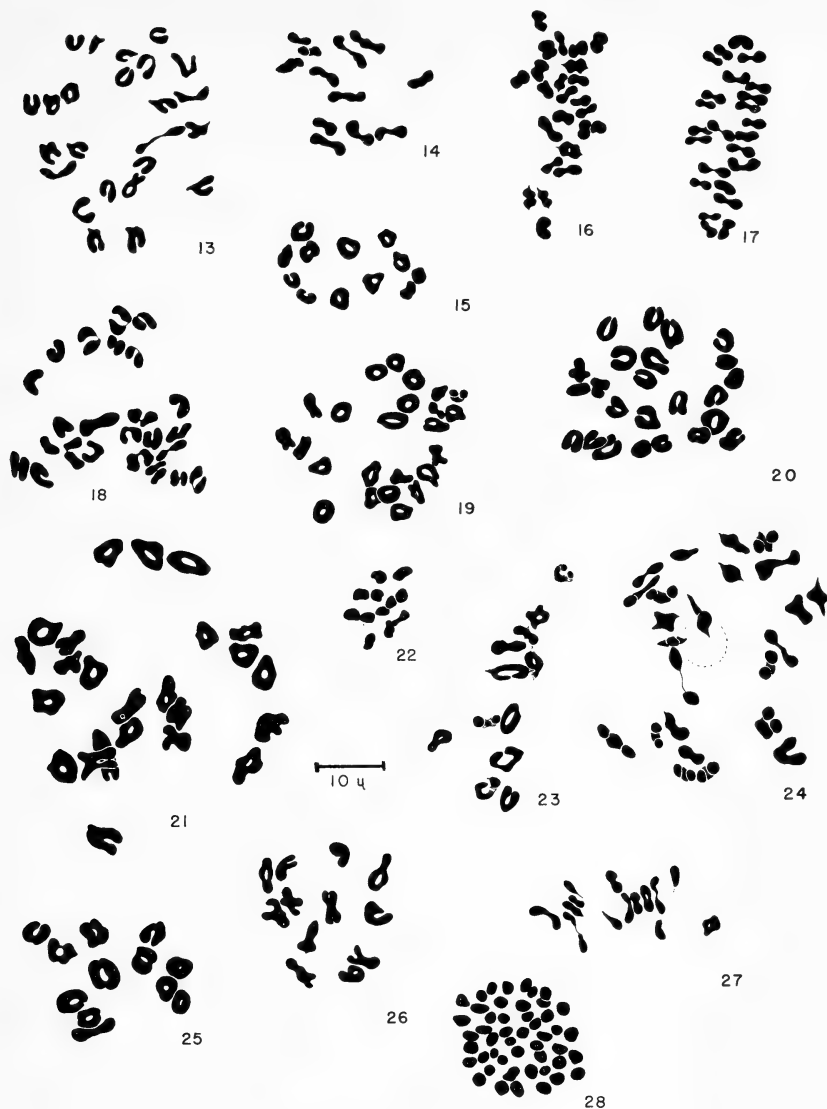
SILENE CALIFORNICA Durand. $2n=48$. Tetraploid. CALIFORNIA. Tulare County: Echo Point, near Moro Rock, Sequoia National Park, *Kruckeberg 3394*. Mendocino County: 4 miles north of Laytonville on U. S. Highway 101, *Kruckeberg 3918*.

SILENE CALIFORNICA Durand. $2n=72$. Hexaploid. CALIFORNIA. Del Norte County: gravel bar along Smith River at Gasquet, *Kruckeberg 3919*.

SILENE CAMPANULATA Wats. $2n=48$. CALIFORNIA. Siskiyou County: 12 miles southwest of Etna on Somes Bar road, *Hitchcock 20237*.

SILENE CLOKEYI H. & M. $2n=96$. NEVADA. Clark County: along ridge, 2 miles from summit of Charleston Peak, *Kruckeberg 3911*.

SILENE DOUGLASII Hook. $2n=48$. CALIFORNIA. Plumas County: rocky flats above Elwell Lake, *Kruckeberg 2897*; rocky flats between Sand Lake and Packer Lake, near Sierra Buttes, *Kruckeberg 3697*. Trinity County: granite talus at Emerald Lake, Trinity Alps, *Kruckeberg 3743*; gravelly alluvium near Portugese Camp between Emerald Lake and Morris Meadows, Trinity Alps, *Kruckeberg 3744*. OREGON. Benton County: grassy summit of Marys Peak, *Kruckeberg 2918*. Multnomah County: Larch Mountain, *Mrs. Mackaness, s.n.*; Bonneville, *Hitchcock s.n.* Clackamas County: ridge 0.5 miles east of Devils Peak, *Kruckeberg 4006*. IDAHO. Idaho County: Indian Hill lookout above Selway River, *Kruckeberg 4095*; granitic slopes above Canteen Meadows, Crags Mountains, *Kruckeberg 4137*; southeastern granitic rim of Crags Mountains, *Kruckeberg 4140*. Valley-Custer county line: rock crevices, Cape Horn Mountain, *Kruckeberg 4177*. Custer County: 2 miles east of Toxaway Lake, Sawtooth Mountains, *Kruckeberg 4198*; talus about Wild Horse Lakes, Mount Hyndman area,



FIGS. 13-28. Chromosomes of *Silene* microsporocytes. FIG. 13. *S. thurberi*, Diak. (Kruckeberg 3863). FIG. 14. *S. williamsii*, I M (Donnelly Dome, Gjaerevoll, s.n.). FIG. 15. *S. antirrhina*, Diak. (Palmer, s.n.). FIG. 16. *S. caroliniana*, I M (Channell, s.n.). FIG. 17. *S. caroliniana wherryi*, I M (Epstein, s.n.). FIG. 18. *S. polypetala*, Diak. (Galle, s.n.). FIG. 19. *S. regia*, Diak. (G. W. Carver National Monument, Palmer, s.n.). FIG. 20. *S. rotundifolia*, Diak. (Sherman, s.n.). FIG. 21. *S. subciliata*, Diak. (Dormon, s.n.). FIG. 22. *Lychnis wilfordii*, II M (Alpine Garden Society 1280). FIG. 23. *Silene keiskei*, I M (Mount Ho-o, Ozawa, s.n.). FIG. 24. *S. repens latifolia*, Diak. (Roberson, s.n.). FIG. 25. *S. struthiloides*, Diak. (Bryan, s.n.). FIG. 26. *Silene* sp., Diak. (Stainton Sykes & Williams 8108). FIG. 27. *Silene* sp., I M (Stainton Sykes & Williams 8178). FIG. 28. *S. wrightii*, I M, Kruckeberg 4716. Diak., diakinesis; I M, first metaphase; II M, second metaphase.

Kruckeberg 4252. WASHINGTON. Chelan County: Basalt ridge above Liberty, *Kruckeberg* 4209; Icicle Creek, *Hitchcock* 20190. Okanogan County: between Twisp and Omak on Loup-Loup highway, *Kruckeberg* 3274; summit of Loup-Loup highway, *Kruckeberg* 3276; 5 miles west of Wauconda on highway to Republic, *Kruckeberg* 3279. Skamania County: 1 mile southeast of Timberline Camp on Timberline Trail, Mount Saint Helens, *Kruckeberg* 3992. Stevens County: summit of Chewelah ski lift on road to Chewelah Peak, *Kruckeberg* 4052; between ski lift summit and Chewelah Peak, on open ridges, *Kruckeberg* 4057.

SILENE GRAYI Wats. 2n=48. CALIFORNIA. Trinity County: between Deer Creek basin and Deer Lake, Trinity Alps, *Kruckeberg* 3759; between Deer Creek Pass and Stonewall Pass, Trinity Alps, *Kruckeberg* 3766; 3.5 miles above Trinity Alps resort on Red Mountain trail below Stonewall Pass, *Kruckeberg* 3772.

SILENE HOOKERI Nutt. ex T. & G. 2n=72. OREGON. Benton County: between Kings Valley and Wren, *Kruckeberg* 2697. Douglas County: 5 miles up Little River, south of Glide, *Cohen s.n.* Josephine County: peridotite alluvium bordering Whiskey Creek, 3 miles west of Obrien, *Kruckeberg* 3777.

SILENE INVISA H. & M. 2n=48. CALIFORNIA. Plumas County: rocky flats above Elwell Lake, Lakes Basin area, *Kruckeberg* 2897b; rocky swales above Upper Tamarack Lake, Sierra Buttes area, *Kruckeberg* 3694. Trinity County: wooded slope between Deer Creek basin and Deer Lake, Trinity Alps, *Kruckeberg* 3759a.

SILENE LACINIATA Cav. subsp. *MAJOR* H. & M. 2n=96. CALIFORNIA. Los Angeles County: west of Beverly Glen Canyon on Mulholland Drive, Santa Monica Mountains, *Snow s.n.*; Turnbull Canyon, Whittier, *Raven s.n.* San Diego County: 0.5 mile east of Potrero Store along State Highway 94, *Walters s.n.* Santa Barbara County: Bishop Ranch, *Clarke s.n.*

SILENE LACINIATA Cav. subsp. *GREGGII* (Gray) H. & M. 2n=48. ARIZONA. Apache County: at crossing of west fork Little Colorado River, between Greer and junction with Highway 73, *Kruckeberg* 4608. Cochise County: along Rustler Park road, Chiricahua Mountains, *Kruckeberg* 3862; rocky banks of Cave Creek, at Herb Martyr Forest Camp, Chiricahua Mountains, *Kruckeberg* 3863; between Rustler Park and Barfoot Lookout, *Kruckeberg* 4643; Crest Trail to Fly Peak, south of Rustler Park, Chiricahua Mountains, *Kruckeberg* 4650. Graham County: rocky slopes, 4 miles below Hospital Flats, Graham Mountains, *Kruckeberg* 3878. NEW MEXICO. Catron County: ten miles northeast of Collins Park on road to Datil, *Kruckeberg* 4703. Grant County: rocky slopes overlooking copper mines at Santa Rita, *Kruckeberg* 4721. TEXAS. Brewster County: between Boot Springs and pass overlooking Inner Basin, Big Bend National Park, *Kruckeberg* 4776.

SILENE LEMMONII Wats. 2n=48. CALIFORNIA. Tulare County: above Lodgepole Camp on road to corral, Sequoia National Park, *Kruckeberg* 3393. Tuolumne County: grade east of Yosemite Creek along Tioga Pass Road, *Kruckeberg* 3530. Sierra County: along State Highway 89 at Calpine Lookout road, *Kruckeberg* 3667. Plumas County: woods at junction of Susanville and Lake Almanor roads, State Highway 89, *Kruckeberg* 3702. San Bernardino County: woods along road from South Fork of Santa Ana River to Barton Flats, *Kruckeberg* 3846.

SILENE MARMORENSIS Kruck. 2n=48. CALIFORNIA. Siskiyou County: one mile north of Somes Bar on road to Camp Three, *Hitchcock* 20221, type.

SILENE MENZIESII Hook. 2n=24. Diploid. CALIFORNIA. Fresno County: Jackass Meadows Forest Camp, below Florence Lake, *Kruckeberg* 3436. IDAHO. Custer County: 2 miles above Wild Horse Creek Forest Camp, *Kruckeberg* 4265.

SILENE MENZIESII Hook. 2n=48. Tetraploid. OREGON. Wallowa County: Evergreen Forest Camp, upper Imnaha River, *Kruckeberg* 3120. CALIFORNIA. Trinity County: upper end of Morris Meadows, Stuart Fork of Trinity River, Trinity Alps, *Kruckeberg* 3746. IDAHO. Valley County: lower Bear Valley at Poker Meadows Campground, *Kruckeberg* 4192. Custer County: Wild Horse Creek Forest Camp, *Kruckeberg* 4292. Bear Lake County: on tailings of phosphate mine, west slope of Snowdrift Mountain, *Kruckeberg* 4527. Custer County: 10 miles west of Challis, on talus of upper

Daugherty Gulch, *Kruckeberg* 4542. WASHINGTON. Chelan County: 1 mile east of U. S. Highway 10 on State Highway 15C to Lake Wenatchee, *Kruckeberg* 3259. Kittitas County: along Swauk Creek, $\frac{1}{8}$ mile below Liberty Guard Station, *Kruckeberg* 3010; base of Iron Peak trail, North Fork Teanaway River, *Kruckeberg* 3289. Okanogan County: rocky alluvium of Methow River, 2 miles below Mazama, *Kruckeberg* 3273; Sweat Creek Forest Camp, 7 miles west of Republic, *Kruckeberg* 3283. Stevens County: along trail between Calispell Meadows and Calispell Peak, *Kruckeberg* 4081.

SILENE MONTANA Wats. 2n=48. CALIFORNIA. Tuolumne County: along Tioga Pass road between Tamarack Flats and Yosemite Creek, *Kruckeberg* 3529. Shasta County: between Chaos Jumbles and Noble Pass, Lassen Volcanic National Park, *Kruckeberg* 3713. OREGON. Klamath County: slopes above Rim Drive, 3 miles above Park Headquarters, Crater Lake National Park, *Kruckeberg* 3780. NEVADA. Ormsby County: along U. S. Highway 50, east of Spooner Summit, 10 miles west of Carson City, *Kruckeberg* 3652.

SILENA NUDA (Wats.) H. & M. 2n=48. CALIFORNIA. Sierra County: 1 mile east of Calpine on road to Beckwourth, *Kruckeberg* 3664. Plumas County: 1 mile west of Portola along U. S. Highway 40, *Kruckeberg* 3669; 3 miles northwest of Lake Almanor along State Highway 89, *Kruckeberg* 3700.

SILENE NUDA (Wats.) H. & M. subsp. INSECTIVORA (Hend.) H. & M. 2n=48. OREGON. Klamath County: Sprague River valley, 7.5 miles west of Bly along State Highway 66, *Kruckeberg* 4030 (type locality).

SILENE OCCIDENTALIS Wats. 2n=48. CALIFORNIA. Sierra County: timbered rocky flats between Sand Lake and Packer Lake, Sierra Buttes area, *Kruckeberg* 3696.

SILENE OREGANA Wats. 2n=48. IDAHO. Valley County: Lodgepole pine flats 5 miles west of McCall on highway to New Meadows, *Kruckeberg* 4151.

SILENE PARISHII Wats. 2n=48. CALIFORNIA. San Bernardino County: Grout Bay, Big Bear Lake, *Everett* 8248, *Kruckeberg* 3831; 2 miles above road's end, along trail to Mount San Gorgonio, *Kruckeberg* 3848.

SILENE PARRYI (Wats.) H. & M. 2n=48. Tetraploid. IDAHO. Bear Lake County: open, west-facing slopes of Snowdrift Mountain, *Kruckeberg* 4520. WASHINGTON. Chelan-Kittitas County line: Mount Lilian, eastern Wenatchee Mountains, *Kruckeberg* 3229, 3232. Stevens County: between head of ski lift and summit, Chewelah Peak road, *Kruckeberg* 4056; $\frac{3}{4}$ mile below lookout, Chewelah Peak, *Kruckeberg* 4064; southwest-facing slopes of Calispell Peak, *Kruckeberg* 4072; open ridge $\frac{3}{4}$ mile south of Calispell Peak, *Kruckeberg* 4079. MONTANA. Flathead County: east slopes of Mount Aeneas, Swan River Range, *Kruckeberg* 4306. Glacier National Park: just south of Logan Pass, on rocky ledges of "Hanging Gardens," *Kruckeberg* 4340. CANADA. Waterton Lakes National Park, Alberta: east-facing slope above upper Carthew Lake, on trail between Cameron Lake and Waterton Lake, *Kruckeberg* 4366.

SILENE PARRYI (Wats.) H. & M. 2n=96. Octoploid. WASHINGTON. Clallam County (Olympic National Park): at Idaho Shelter, Hurricane Ridge, *Kruckeberg* 2776, 4045; along ridge to Mount Angeles, *Kruckeberg* 2792; along trail to Moose Lake from Obstruction Point, *Kruckeberg* 4048. Kittitas County: alluvial flats at Fish Lake, upper Cle Elum River, *Kruckeberg* 3221; at base of Iron Peak trail, North Fork of Teanaway River, *Kruckeberg* 3288; along upper reaches of Miller Peak trail, *Kruckeberg* 3967.

SILENE PETERSONII Maguire. 2n=96. UTAH. Garfield County: on slopes of red talus and clay, 5.5 miles east of U. S. Highway 89, on Red Canyon road to Bryce Canyon National Park, *Kruckeberg* 3904. Iron County: limestone clay along west-facing rim of Cedar Breaks, *Kruckeberg* 3908.

SILENE REPENS Patrin. subsp. AUSTRALE H. & M. 2n=24. Diploid. IDAHO. Custer County: Boulder Creek, 5 miles above Wildhorse Creek Canyon, *Kruckeberg* 4286a; Boulder Creek basin, 0.5 mile below Boulder Lake, *Kruckeberg* 4290.

SILENE SARGENTII Wats. 2n=48. CALIFORNIA. Fresno County: pass between upper Bear Creek Meadow and Rose and Marie Lakes, *Kruckeberg* 3459; at Marie Lake,

Kruckeberg 3482. Shasta County: near summit of Lassen Peak, Lassen Volcanic National Park, *Kruckeberg* 3711.³

SILENE SCAPOSA Robins. 2n=48. OREGON. Harney County: 1 mile north of Squaw Butte on dirt road to U. S. Highway 20 (Burns-Bend highway), *Kruckeberg* 4031.

SILENE SCOULERI Hook. 2n=48. IDAHO. Benewah County: between Tensed and Potlatch on U. S. Highway 95, *Kruckeberg* 4085.

SILENE SPALDINGII Wats. 2n=48. WASHINGTON. Garfield County: near Colton, *Daubenmire s.n.*

SILENE THURBERI Wats. 2n=48. ARIZONA. Cochise County stony alluvium along Cave Creek at Herb Martyr Forest Camp, Chiricahua Mountains, *Kruckeberg* 3863.

SILENE VERECUNDA Wats. subsp. *VERECUNDA* 2n=48. CALIFORNIA. San Francisco County: rocky soil at east end of summit ridge of Mount Davidson, *Raven s.n.*

SILENE VERECUNDA Wats. subsp. *ANDERSONII* (Clokey) H. & M. 2n=48. NEVADA. Clark County: rocky alluvium of Kyle Creek canyon, 1 mile below Charleston Park, Charleston Mountains, *Kruckeberg* 3915.

SILENE VERECUNDA Wats. subsp. *PLATYOTA* (Wats.) H. & M. 2n=48. CALIFORNIA. Tulare County: Last Chance Meadows area, Sierra Nevada Range, *Kruckeberg* 3345; 7 miles above California Hot Springs on road to Johnsdale, *Kruckeberg* 3392; 5 miles west of Hockett Meadows, Sequoia National Park, *Kruckeberg* 3422a. Los Angeles County: north slope of Mount Waterman, San Gabriel Mountains: *Kruckeberg* 3821; Horse Flats, San Gabriel Mountains, *Kruckeberg* 3822; north-facing slopes of Blue Ridge, San Gabriel Mountains, *Kruckeberg* 3916. San Bernardino County: 5 miles below Lake Arrowhead on State Highway 18; flats above Moon Ridge, south side of Bear Valley on road to south fork Santa Ana River, *Kruckeberg* 3840 (eglandular form); near summit of Sugarloaf Ridge, 6 miles southeast of Bear Valley, *Kruckeberg* 3843 (eglandular form). Riverside County: 3.4 miles south and east of State Highway 74, Bautista Canyon, *Vasek s.n.*

SILENE WILLIAMSI Britt. 2n=24. ALASKA. Slopes of Shaw Creek, Richardson Highway, *Gjaerevoll* 1444; heath, Donnelly Dome, Alaska Range, *Gjaerevoll* 1284.

SILENE WRIGHTII Gray. 2n=96. NEW MEXICO. Grant County: in crevices of massive boulders at base of sheer rock cliffs, overlooking copper mines at Santa Rita, *Kruckeberg* 4716.

EASTERN NORTH AMERICAN SPECIES

SILENE ANTIRRHINA L. 2n=24. MISSOURI. Jasper County: near Webb City, *Palmer s.n.*

SILENE CAROLINIANA Walt. 2n=48. NORTH CAROLINA. Franklin County: 9 miles east of Wake Forest, granitic "flat-rock" area, *Channell s.n.* Orange County: Chapel Hill, *Bell s.n.*

SILENE CAROLINIANA Walt. subsp. *WHERRYI* (Small) Clausen. 2n=48. Garden culture: Larchmont, New York, *Epstein s.n.*

SILENE POLYPETALA (Walt.) Fern. and Schub. 2n=48. GEORGIA. Talbot County: north of county bridge, hillside above Flint River, *Galle s.n.*

SILENE REGIA Sims. 2n=48. MISSOURI. Dade County: near South Greenfield, *Palmer s.n.* Newton County: George Washington Carver National Monument, *Palmer s.n.*

SILENE ROTUNDIFOLIA Nutt. 2n=48. TENNESSEE. Marion County: crevices of the "Chimneys," gorge of Pocket Creek, Whitwell Pocket area, *Sherman s.n.*

SILENE STELLATA (L.) Ait. [including *S. scabrella* (Nieuwl.) Palm. and Steyer.] 2n=48. INDIANA. Starke County: *Jackson s.n.* MISSOURI. Newton County: near Diamond, George Washington Carver National Monument, *Palmer s.n.* KANSAS. Riley County: 40 miles east of Aurora, woods along Fancy Creek, *Fraser*. WEST VIRGINIA. Monongalia County: on Permian shale banks, vicinity of Morgantown, *Constable & Core s.n.* LOUISIANA. northwestern portion of state, *Dormon s.n.*

³ Plants intermediate between *S. sargentii* and *S. Suksdorfii* Robins.

SILENE SUBCILIATA Robins. $2n=48$. LOUISIANA. "Western Louisiana," *Dormon s.n.* (garden culture).

SILENE VIRGINICA L. $2n=48$. NORTH CAROLINA. Wake County: 18 miles north of Raleigh, across the Neuse River, on State Highway 50, *Smith s.n.*

SPECIES OUTSIDE CONTINENTAL NORTH AMERICA

LYCHNIS WILFORDII Maxim. $2n=24$. JAPAN: Garden culture, *M. Ozawa s.n.*; garden culture, *Alpine Garden Society 1280*.

PETROCOPTIS PYRENAICA Braun. $2n=24$. EUROPE. Garden culture, *Museum of Natural History, Paris s.n.*

SILENE KEISKEI Miq. $2n=24$. JAPAN: Mt. Ho-o, *M. Ozawa s.n.*; Mt. Kitadake, *Ozawa s.n.*

SILENE REPENS Patrin. var. LATIFOLIA Turcz. $2n=48$. JAPAN: Garden culture, *Mrs. L. N. Roberson s.n.*; garden culture, *Epstein s.n.*

SILENE STRUTHIOLOIDES Gray. $2n=24$. HAWAII. Hawaii: near the Kilauea Crater, Hawaii National Park, *Bryan s.n.*

SILENE species. $2n=24$. NEPAL: Tegar, north of Mustang, *Sykes & Williams 8108*; Larjung, south of Tukucha, Kali Gandaki Valley, *Sykes & Williams 8178*.

Department of Botany,
University of Washington, Seattle

LITERATURE CITED

- HITCHCOCK, C. L., and B. MAGUIRE. 1947. A revision of the North American species of *Silene*. Univ. Wash. Publ. Biol. 13:1-73.
- KRUCKEBERG, A. R. 1954. Chromosome numbers in *Silene* (Caryophyllaceae): I. *Madroño* 12:238-246.
- . 1955. Interspecific hybridizations of *Silene*. *Am. Jour. Bot.* 42:373-378.
- . 1960. A new *Silene* from northwestern California. *Madroño* 15:172-177.

A NEW SPECIES OF ZINNIA FROM MEXICO

A. M. TORRES

During the course of a cytotaxonomic study of the genus *Zinnia* (Compositae), plants started from seeds kindly provided by Dr. Jerzy Rzedowski of the Universidad Autónoma de San Luis Potosí, México, were cultivated in the greenhouses of Indiana University. One collection, when grown to maturity, proved to be a new species known thus far only from the area where the seeds were collected.

***Zinnia citrea* sp. nov.** Planta perennis, cespitosa, ad 2 dm. alta; caulis viridibus, strigosis; foliis oppositis, amplexicaulibus, uninervis, linearibus, ad 3.5 cm. longis, 0.8-1.9 mm. latis, sparse strigosis aut glabrescentibus, sparse glanduloso-punctatis; capitulis terminatibus in pedunculis 0.8-2.0 cm. longis, subhemisphaericis, 0.4 cm. latis 0.5 cm. altis; phyllariis oblongis, firme-gradatis, herbaceis, minuto-glanduliferis, apicibus obtusis, ciliatis; radiis ca. 7, chloreis oblongis, ad 0.8 cm. longis 0.5 cm. latis, sine tubo, in dorso viridis nervis, apicibus 0.3 lobis; achaeniis radorum oblanceolatis, ad 4.2 mm. longis, tuberculatis, nigrescentibus, sine aristis; floribus disci ca. 22, tubis 3.1 mm. longis, lobis 1.4 mm.

longis, intus lobis lanuginosis, supra flavo-viridibus, infra viridibus; achaeniis disci oblanceolatis, compressis, ad 2.6 mm. longis, sparse ciliatis vel vere glabris, marginibus ciliatis, pappis 2 inaequalis aristatis; receptaculi paleis lanceolatis, scariosis, apicibus acutis minuto-dentatis, plus minusve viridibus; receptaculis convexis.

Plants perennial, caespitose, about 2 dm. high; stems green, strigose; leaves opposite, sheathing, one-nerved, linear, about 3.5 cm. long, 0.8–1.9 mm. wide, sparsely strigose or becoming glabrous, attenuate, sparsely glandular-punctate; heads terminal on peduncles 0.8–2.0 cm. long, sub-hemispherical, 0.4 cm. wide, 0.5 cm. high; phyllaries oblong, strongly graduated, herbaceous, apices obtuse, ciliate, minutely glandular; rays about 7, lemon-colored, oblong, about 0.8 cm. long, 0.5 cm. wide, tubelless, green-nerved on the back, apices 0–3 lobed; ray achenes oblanceolate, about 4.2 mm. long, tuberculate, becoming black, awnless; disk flowers about 22, the tube 3.1 mm. long, the lobes 1.4 mm. long, velvety on inner surface, yellow-green above, green below; achenes of the disk oblanceolate, compressed, 2.6 mm. long, sparsely ciliate or essentially glabrous, the margins ciliate, the pappus of 2 unequal awns; pales of the receptacle lanceolate, scarious, the apices acute, minutely dentate, more or less green; receptacle convex.

Type. Mexico. Seed collected near Santo Domingo, municipality of Guadalupe, San Luis Potosí, on deep alluvial soil with *Prosopis*. Elev. 1200 m. Cultivated in greenhouse, Indiana University, 1959, *Torres 139* (IND).

Zinnia citrea is very closely allied morphologically, but entirely distinct from *Z. grandiflora* Nutt. and *Z. acerosa* (DC.) Gray (considered by the writer to include *Z. pumila* Gray). *Zinnia grandiflora* occurs in the southwestern United States as far north as Kansas, and in the Mexican states of Sonora, Chihuahua, Coahuila and Durango. *Zinnia acerosa* is found in the southern parts of Arizona and New Mexico, western Texas, and the adjacent portions of México as far south as Durango, Zacatecas and San Luis Potosí.

Some of the differences between the three species are indicated below.

	<i>Z. citrea</i>	<i>Z. acerosa</i>	<i>Z. grandiflora</i>
Number of leaf nerves	1	1	3
Ray color	lemon	white	yellow
Number of rays	5–7	4–6	3–6
Number of disk flowers	18–25	8–13	18–24
		n = 10	n = 21
Chromosome no.	n = 20	n = 19	2n = 42
		n = 20	

Compared with *Z. citrea*, the rays of *Z. grandiflora* are yellow, usually fewer and considerably larger; the disk is red or sometimes green, instead of yellowish; the leaves are wider and longer but quite variable; the somatic chromosome number is 42. Jackson (1959) has reported a gametic chromosome number is 21 and the somatic chromosome number

is 42. Jackson (1959) has reported a gametic chromosome number of 24 for *Z. grandiflora*. The rays of *Z. acerosa* are white (drying pale yellow), generally fewer, slightly larger and the disk is reddish. Populations having gametic chromosome numbers of 10, 19, and 20 have been found. Voucher herbarium specimens for the chromosome counts are deposited at Indiana University.

Department of Botany
Indiana University
Bloomington, Indiana

LITERATURE CITED

JACKSON, R. C. 1959. Documented chromosome numbers of plants. *Madroño* 15:52.

A COMMENT ON COLD SUSCEPTIBILITY OF PONDEROSA AND JEFFREY PINES

WILLIS W. WAGENER¹

Dr. Haller's recent paper² on factors affecting the distribution of ponderosa and Jeffrey pines prompts a supplementary note concerning the comparative effects of low temperatures observed on the two species in northeastern California. In this region extensive mixed stands of the two occur, many of them above the 5,000-foot level, providing a convenient comparison of their reactions to environmental conditions for the geographical races represented there.

Dr. Haller considers that *Pinus jeffreyi* is more tolerant than *P. ponderosa* of extremes of low temperature and aridity, but he concludes that the differential limiting effect of low temperature must be exerted in the seedling stage or on young trees because mature trees of *P. ponderosa* at its upper altitudinal limit appear vigorous and show no evidence of stunting. My observations over the past 25 years, following periods of severe cold, fail to indicate any material difference between the two species in their ability to withstand extreme cold, either as young or mature trees.

In January 1937, California experienced two very cold periods, particularly east of the Sierra Nevada crest. The first of these was from January 8 to 10 and the second from January 20 to 25. The lowest temperature reported to the United States Weather Bureau for these periods in California was -45°F . at Boca, California, on January 20.

Early in February a belt of pronounced damage to pines and other vegetation became noticeable along the east face of the Sierra Nevada for almost its entire length. At the north end it was narrow, from 25 to

¹ Forest Pathologist, Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture.

² Haller, John R. Factors affecting the distribution of ponderosa and Jeffrey pines in California. *Madroño* 15:65-71. 1959.

200 yards wide, depending on slope, and occurred at an elevation of about 4,800 feet. Toward the south the belt was wider and was located at a gradually increasing elevation, between 7,000 and 8,000 feet at the south end.

From the Truckee River southward the damage to pines consisted largely of foliage browning, from which practically all the trees later recovered. On the slope above Long Valley Creek, Lassen County, however, damage was much more pronounced, and many mature pines, as well as trees of younger ages, failed to recover. Mortality in the pines ran as high as 75 percent.

In the topographic gap created by the Susan River the belt-like character of the zone of damage was less evident but the major injury was found at approximately the same elevation as above Long Valley Creek. A strong temperature inversion apparently occurred at this level. On low benches along the Susan River a number of cases were observed where the lower foliage of young Jeffrey pines 20 to 30 feet in height was almost completely killed, whereas that of the upper crowns on the same trees was only slightly damaged. In addition, many of the trees showed browning of the phloem tissues of the inner bark of the lower trunks and branches. Most of these trees died later. The immediate cause of death appeared to be the activities of bark insects attracted by the killed phloem. Whether the trees could have survived in the absence of the insects was not determined.

In Jeffrey pine the spread between noticeable injury to foliage and the complete killing of foliage and branches or trunks appeared to be very much narrower than in ponderosa pine. Cases were noted in which foliage on ponderosa pines was almost completely killed, but nearly all buds and twigs remained alive and produced fairly good growth the following season. This was not true for Jeffrey pines. In them, severe foliage injury was accompanied by severe bark injury, and no recovery followed. Where both species were present in the same location there was less mortality in the ponderosa than in the Jeffrey pines.

Another series of abnormally low temperatures prevailed in California in January, 1949. Minima of -38°F. were registered at Boca, California, on the 25th and of -31°F. at Alturas and Bridgeport Dam on the 26th.

Damage to pines on low ground east of the Sierra Nevada as a result of this series of cold waves during the month was much more general in occurrence than in 1937. Heavy browning of foliage of young ponderosa and Jeffrey pines on the borders of low flats or along stream bottoms was noted in interior basin drainages from Modoc County to the San Bernardino Mountains. Stringers of pines along stream courses extending into the Honey Lake and Carson valleys were heavily damaged, and many trees eighteen to twenty inches in diameter breast high later succumbed. These were mostly Jeffrey pines but some ponderosa pines were present also. Mortality in them appeared to be no greater in proportion than in the Jeffrey. Recovery in young trees appeared to depend on whether or

not the inner bark tissues of the main stem had been injured. Killing of these tissues was found both in ponderosa and Jeffrey pines, with later mortality after the stems had been invaded by bark-feeding insects.

Neither in 1937 nor in 1949 was enough difference in mortality from the abnormal cold noted between established trees of the two species to account for the tendency of Jeffrey pine to be confined to the higher elevations or colder situations. If an ecologically significant difference exists between the two with respect to cold tolerance it must be operative in the seedling stage, as Haller suggests, or through some other influence than differential mortality from cold.

DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See MADROÑO 9:257-258. 1948)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
RANUNCULACEAE				
<i>Delphinium carolinianum</i> Walter	n = 8	B. L. Turner, TEX ¹	Thompson & Turner 96 TEX	Hardin County, Texas
<i>virescens</i> var. <i>macroceratilis</i> (Rydb.) Ewan	n = 8	B. L. Turner, TEX	Turner 4395 TEX	Bexar County, Texas
SAXIFRAGACEAE				
<i>Saxifraga ferruginea</i> Graham	n = 19	K. I. Beamish, UBC	Beamish 7828 UBC Beamish 9000 UBC	Mt. Seymour near Vancouver, B.C., Canada Caulfeilds, near Vancouver, B.C., Canada
<i>integrifolia</i> Hook.	n = 19	K. I. Beamish, UBC	Beamish 7057 UBC Beamish, Vrugtman & Sparling 8017 UBC	Thetis Lake, Vancouver Island, B.C., Canada Elk Falls, Vancouver Island, B.C., Canada
<i>montanensis</i> Small	n = 19	K. I. Beamish, UBC	Vrugtman, Beamish & Kallio 9027 UBC	Princeton-Merritt Road, B.C., Canada
<i>occidentalis</i> Watson sensu lat.	n = 19	K. I. Beamish, UBC	Beamish, Vrugtman & Sperrings 8224, UBC	Botanie Valley, near Lytton, B.C., Canada

¹ Symbols for institutions are those listed by Lanjouw and Stafleu. Index Herbariorum, Part I. Second edition, 1954, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>Saxifraga tolmiei</i> T. & G.	n = 15	K. I. Beamish, UBC	<i>Beamish 7831</i> UBC	Mt. Seymour near Vancouver, B.C., Canada
UMBELLIFERAE <i>Pseudotaenidia montana</i> Mackenz.	2n = 22	R. L. Guthrie WVA	<i>Guthrie</i> s.n. UC	Greenbrier County, W. Va.
GARRYACEAE <i>Garrya lindheimeri</i> Torr.	n = 11	B. L. Turner, TEX	<i>Turner 3967</i> TEX	Austin, Travis County, Texas
VERBENACEAE <i>Verbena hastata</i> L.	n = 7	J. D. Poindexter, KANU	<i>Poindexter 33</i> KANU	Douglas County, Kansas
<i>bracteata</i> Lag. & Rodr.	n = 7	R. C. Jackson, KANU	<i>Poindexter 18</i> KANU	Trego County, Kansas
<i>stricta</i> Vent.	n = 7	J. D. Poindexter, KANU	<i>Poindexter 37</i> KANU	Douglas County, Kansas
<i>urticifolia</i> L.	n = 7	J. D. Poindexter, KANU	<i>Poindexter 9</i> KANU	Douglas County, Kansas
SCROPHULARIACEAE <i>Penstemon clutei</i> A. Nels.	n = 8	R. C. Jackson, KANU	<i>R. C. & S. W. Jackson 2683-1</i> KANU	Coconino County, Arizona
COMPOSITAE <i>Blennosperma nanum</i> (Hook.) Blake var. <i>robustum</i> Howell	n = 7	R. Ornduff, UC	<i>Ornduff 4963</i> UC	Pt. Reyes, Marin County, California
<i>Encelia frutescens</i> Gray	n = 17	R. C. Jackson, KANU	<i>Jackson 2684</i> KANU	Coconino County, Arizona
<i>Haplopappus havardii</i> Waterfall	n = 4	R. C. Jackson, KANU	<i>Jackson 2717</i> KANU	Lea County, New Mexico
<i>phyllocephallus</i> DC. subsp. <i>phyllo-</i> <i>cephalus</i>	n = 6	R. C. Jackson, KANU	<i>Jackson 2610</i> KANU	Cameron County, Texas
<i>phyllocephalus</i> subsp. <i>annuus</i> (Rydb.) Hall	n = 6	R. C. Jackson, KANU	<i>Ungar 729</i> KANU	Stafford County, Kansas
<i>spinulosus</i> (Pursh) DC. subsp. <i>spinulosus</i>	n = 4+1	R. C. Jackson, KANU	<i>Jackson 2455-1</i> KANU	Socorro County, New Mexico
<i>spinulosus</i> (Pursh) DC. subsp. <i>spinulosus</i>	n = 4+2	R. C. Jackson, KANU	<i>Jackson 2455-14</i> KANU	Socorro County, New Mexico

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>Machaeranthera blephariphylla</i> (Gray) Shinnars	2n = 8	R. C. Jackson, KANU	<i>Jackson 2901</i> KANU	Durango, Mexico
<i>tagetina</i> Greene	n = 4	R. C. Jackson, KANU	<i>Jackson 2600</i> KANU	Hidalgo County, New Mexico
<i>Porophyllum scoparium</i> Gray	n = 12	R. C. Jackson, KANU	<i>R. C. & S. W. Jackson 2701</i> KANU	Otero County, New Mexico
<i>Psilostrophe cooperi</i> (Gray) Greene	n = 16	R. C. Jackson, KANU	<i>R. C. & S. W. Jackson 2693</i> KANU	Yavapai County, Arizona
<i>Sclerocarpus uniserialis</i> (Hook.) Benth. & Hook. f.	n = 12	B. L. Turner, TEX	<i>Turner et al. 3313</i> TEX	Jackson County, Texas
<i>Viguiera adenophylla</i> Blake	n = 17	C. B. Heiser, IND	<i>Stoutamire 2813</i> IND	North of San Luis Potosí-Nuevo Leon state line, Mexico
<i>deltoidea</i> var. <i>Parishii</i> (Greene) Vasey & Rose	n = 18	C. B. Heiser, IND	<i>Neher in 1958</i> IND	Near Palm Springs, Riverside County, California
<i>dentata</i> var. <i>brevipes</i> (DC.) Blake	n = 17	B. L. Turner, TEX	<i>Turner 4463B</i> TEX	Austin, Travis County, Texas
<i>porteri</i> (A. Gray) Blake	n = 17	C. B. Heiser, IND	From seed (<i>Duncan</i>) <i>Heiser 4561</i> IND	DeKalb County, Georgia
<i>stenoloba</i> Blake	n = 17	C. B. Heiser, IND	From seed <i>Tucker 3131</i>	Eddy County, New Mexico

REVIEW

Carex—Its Distribution and Importance in Utah. By MONT E. LEWIS. Brigham Young University Science Bulletin, Biological Series 1(2):1-43. 1958. \$1.00.

"The purpose of this report is to bring available information concerning the *Carex* species in Utah up to date." With these modest words Mr. Lewis of the United States Forest Service intermountain regional office in Ogden, Utah, introduces his excellent and original study of the identification, distribution, ecology, and grazing values of Utah carices.

Since the only Utah flora, namely Tidestrom's, is now over a third of a century old, a modern study such as this is most welcome. It is doubly welcome in that it comes from a representative of the federal organization which spends more man-hours interpreting the native plant cover of Utah than any other group. It is gratifying that a man primarily concerned with administration should take the time to produce a work such as this.

The report contains a diagrammatic summary of the mountain physiographic provinces of Utah and of their zonal belts of vegetation. Most interesting floristic, vegetational, and ecological problems are evident from the scattered occurrence of *Pinus ponderosa*, a local intrusion of *Pinus contorta* into the state, a varying amount of pinyon-juniper vegetation in different provinces, a constantly present but supposedly seral aspen-fir belt, and scattered alpine vegetation. Descriptions as well as explanations of most of these phenomena are still lacking in the botanical literature. For subsequent editions we hope Mr. Lewis will find time and opportunity to prepare altitude scales to this zonal vegetation diagram and to characterize the plant communities and floras concerned.

Although the physiographic units used certainly make far more sense for describing the distributions of plants within Utah than do county units, floristic units would be best of all. Do the physiographic divisions of Utah coincide with floristic divisions? For those unfamiliar with floras using floristically defined areas to describe plant distributions, reference may be made to the "Flora of the USSR" [cf. Stearn's paper in the New Phytologist 46:61-87, 1947. Note that a new map appears in Volume 18 (1952) of the Flora USSR] and to recent local floras such as those of Tadzhikistan, Kazakhstan, Central Siberia, Leningrad and Murmansk regions, etc. Hylander's new Scandinavian flora and the new Greenland flora employ similar schemes.

Illustrations of named *Carex* species explain the terminology used in the keys. These keys do not exactly duplicate Mackenzie's and are easier to use for identification to section and to species. They require ripe perigynia; so do most *Carex* keys. For this reason A. Neumann's key to the carices of northwest Germany in vegetative condition deserves mention (Mitteil. Floristischsoziologischen Arbeitsgemeinschaft 3:44-77, 1952). Unfortunately, of the 126 taxa keyed by Neumann, only 6 are found among Lewis' 102 taxa. The species descriptions are pertinent and comparable; distinguishing features are frequently mentioned, and here the author uses his field experience to great advantage.

Distribution statements are short but probably adequate, with the Utah areas given in as full detail as present knowledge permits. This present knowledge is so poor as to make a phytogeographer weep, but one result of Lewis' work will be a rapid advance in our knowledge of where various carices do grow. The ecological data are excellent and far better than anything else available. Writers of extra-Utah floras can most profitably use these data for comparisons. Finally, all interested in range management will treasure Lewis' unique notes on forage values.

The monograph closes with an excellent list of local references, a glossary, an index, and a table summarizing for all species their distribution by physiographic provinces, the mountain belt of vegetation in which they occur, their habitat within this belt, their abundance, and geographical distribution.—JACK MAJOR, Botany Department, University of California, Davis.

NOTES AND NEWS

EDWARD LEE GREENE CORRESPONDENCE—Persons interested in the botanical history of the western United States may find material of value in the correspondence of Edward Lee Greene now in the archives of the University of Notre Dame. This file includes letters to Greene over a period of forty or more years of his botanical career. These range from single letters commenting on specimens or requesting information to extensive correspondence from many of the notable figures in botany. This material is available to scholars able to visit the University of Notre Dame. Also microfilm copies of letters can be supplied at about four cents per picture and photostat copies at about forty cents per copy.

The following list includes the names of most correspondents whose letters are in the Greene files at Notre Dame. It is not necessarily complete. Some of the

material is not alphabetically filed and no catalogue is available at present. To indicate the approximate extent of the correspondence from individuals the following scale is used:

- A. one or two letters
- B. approximately five
- C. approximately ten
- D. approximately twenty five
- E. extensive, usually fifty or more

These designations are based on estimates and not on actual counts, and they do not purport to indicate the intrinsic interest or importance of the letters.

Abrams, L. R.	A	Brainerd, E.	D	Davy, J. B.	B
Alderson, R. D.	B	Bramton, E.	A	Day, D. F.	B
Allen, A. A.	A	Brand, Dr.	A	Dayton, W. A.	A
Allison, E. M.	A	Brandegge, K. & T. S.	B	Deam, C. C.	D
Ames, O.	A	Brinton, J. B.	A	Deane, W.	A
Anderson, C. L.	B	Briquet, J.	A	Delafield, M.	A
Andres, H.	A	Britten, J.	A	Derby, G.	A
Andrews, L.	C	Britton, N. L.	D	Dewey, L. H.	A
Arber, Agnes	A	Brown, C. E.	A	Dickson, J. M.	B
Arthur, J. C.	A	Brown, J. S.	A	Dodge, C. K.	D
Atkinson, G. F.	A	Bruckett, G.	A	Donnelly, H. B.	A
Austin, R. M.	C	Buchanan, W. D.	A	Dudley, W. K.	A
Autran, E.	A	Buckenau, F.	A	Duggan, J.	A
		Budworth, G.	A	Dupret, H.	A
Bailey, L. H.	B	Bull, H. R.	A	Dyer, W.	A
Bailey, W. W.	A	Burgess, E. S. & T. J.	A		
Baillon, L.	A	Burglehaus, F. H.	A	Earle, F. S.	A
Baker, C. F.	E	Burkill, I. H.	A	Eastwood, A.	D
Baker, M.	A	Burrall, H. D.	A	Eaton, A. A.	A
Balfour, I. B.	A	Buscalioni, L.	A	Egerton, J. B.	A
Ball, John	A	Bush, B. F.	D	Eggert, H.	A
Bancroft, F. & R.	A	Butler, F. & G.	A	Eggleston, W. W.	A
Barnes, W.	A	Buysman, M.	A	Elliot, W.	A
Barnhart, J. H.	C			Ellis, J. B.	B
Bartlett, H. H.	A	Campbell, D. H.	A	Elmer, A. D. E.	B
Batalin, A.	B	Canby, W. M.	A	Engelmann, Geo.	E
Bates, J. M.	A	Candolle de, Alp.	A	Evermann, B. W.	A
Baxter, M. S.	A	Case, J. H.	A		
Beal, W. J.	A	Chase, A.	A	Farr, E. M.	B
Bebb, M. S.	E	Choate, H.	A	Farwell, O. A.	D
Becker, W.	A	Clarke, F. L.	A	Fawcett, Wm.	A
Beguino, A.	A	Claybrooke, G.	A	Fedde, F.	B
Bell, A. A.	A	Cleveland, D.	C	Fernald, M. L.	B
Benton, L. E.	A	Cockerell, T. D. A.	C	Fischer, T.	A
Bernard, H.	A	Cocks, R. S.	A	Fitzpatrick, T. J.	A
Bessey, E. A.	A	Cole, L. B.	A	Fletcher, J.	D
Bessey, C. E.	C	Conard, H. S.	A	Friedlander, R.	B
Best, G.	A	Cooper, A. J.	A	Fronani, E.	A
Bethel, E.	A	Copeland, E. B.	A		
Bicknell, E. P.	D	Coulter, J. M.	C	Gager, C. S.	A
Bioletti, F.	B	Coville, F. V.	D	Ganong, W.	A
Bissell, C. H.	A	Crawford, J.	A	Garrett, A. O.	A
Blake, A.	A	Cross, E. R.	B	Gates, F. C.	A
Blankinship, J. W.	A	Curtis, G. P.	B	Gautier, G.	A
Blochman, J.	D	Cusick, Wm. C.	B	Gerard, J. N.	B
Blumer, J. C.	D			Gibbons, G.	A
Boardman, S. L.	A	Davidson, A.	B	Gibson, A.	A
Bolander, H. N.	A	Davidson, G.	A	Gormann, M. W.	A
Bonté, J. H.	B	Davidson, J.	B	Grant, G. B.	C

Gray, A.	E	Knuth, R.	A	Piper, C. V.	B
Greenman, J. M.	A	Koehne, E.	A	Pollard, C. L.	B
Gregorson, D.	A	Krautter, L.	A	Pond, C. F.	A
Gregory, E.	A	Kreke, M.	A	Porter, C. E.	B
Grimes, E. J.	A	Kumlein, L.	A	Porter, T. C.	D
Grose, I. F.	A	Kunze, O.	A	Price, C. G.	B
Grout, A. J.	A			Pringle, C. G.	B
Guillou, A.	A	Langlois, A. B.	A		
		Leiberg, J. B.	B	Reed, F.	A
Haberer, J. V.	A	Lemmon, J. G.	A	Robinson, B. L.	C
Harger, E. B.	A	Limberger, W. B.	A	Rose, J. W.	C
Harper, R. M.	A	Lloyd, F. E.	A	Rosendahl, C. O.	C
Hasse, H. E.	A	Lunell, J.	D	Rusby, H. H.	E
Hastings, G.	A	Lyon, W. D.	B	Ruth, A.	B
Havard, V.	A	Lyon, W. S.	A	Rydberg, P. A.	E
Hedrick, U. P.	A				
Heimer, I. A.	A	MacDougal, D.	A	Sargeant, C. S.	B
Heller, A. A.	D	Macfarlane, J. M.	A	Sears, J. H.	A
Henderson, L.	A	Mackenzie, K. K.	A	Shea, C. L.	A
Henry, J. K.	C	MacMillan, C.	B	Sheldon, E. P.	A
Hensen, G.	A	Macoun, John	E	Sherff, E. E.	A
Hill, E. J.	A	Maxwell, C. F.	A	Siegfried, J. P.	A
Hillegass, G. W.	A	Metcalfe, O. B.	B	Small, J. K.	C
Hine, J. S.	A	Millsbaugh, C. F.	B	Smith, C. P.	A
Hitchcock, A. S.	A	Mohr, C.	A	Smith, J. D.	A
Holden, E. S.	A	Morong, T.	A	Sonne, C. F.	B
Hollick, A.	A	Moseley, E. L.	A	Stapf, O.	A
Holm, T.	A	Moyer, L. R.	A	Stone, Wilbur	A
Holmes, J. A.	A	Mueller, Barron F. von	A	Suksdorf, W. N.	C
Holzinger, J. W.	A	Mulford, A. J.	A		
House, H. D.	D			Thornber, J. J.	A
Howe, M. A.	D	Nelson, A.	D	Tracy, J. P.	B
Howell, T.	A	Nelson, E.	A	Trelease, Wm.	B
Huth, E.	A	Nieuwland, J.	D	Turner, J. H.	A
Jaggard, A. L.	A	Ogden, H. V.	A	Underwood, L. M.	B
Jennings, O. E.	A	Olney, S. C.	D	Urban, J.	B
Jepson, W.	D	Orcutt, C. R.	B		
Johnson, R. H.	A	Osterhout, G. E.	B	Vasey, Geo.	B
Jones, M. E.	A				
Jordan, D. S.	A	Parish, S. B.	C	Watson, Lawrence	E
		Parry, C. C.	D	Watson, Sereno	E
Kearney, T. H.	A	Patterson, H. N.	B	Wellington, R.	A
Keller, R.	A	Paull, C. F.	B	Weigand, K. M.	A
Kelsey, F. D.	A	Pearson, G. A.	A	Wilder, C. M.	B
Kennedy, P. B.	A	Peckinpah, L. A. R.	A	Wilson, N. G.	A
Kneipp, L. F.	A	Pennell, F. W.	A	Wooton, E. O.	D
Knight, O. W.	A	Phelps, O. P.	D	Wright, W. G.	A

The undersigned will be happy to supply further information or to try to locate correspondence from individuals not included in this list. ROBERT P. MCINTOSH, Curator, Greene-Nieuwland Herbarium, University of Notre Dame, Notre Dame, Indiana.

UROSPERMUM PICROIDES (L.) SCHMIDT IN BERKELEY. This cichoriaceous Mediterranean plant has apparently become established on a part of the University of California campus which has not been intensively landscaped (*Hall* in 1915, *Mason* in 1943, *Carter* 4109 in 1960). *Urospermum picroides* may be readily recognized by its flat tuberculate achenes with long slender beaks, the ampule-like bases of which are enlarged to a diameter greater than that of the achenes.—ANNETTA CARTER, Department of Botany, University of California, Berkeley.

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$6.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany

University of California, Berkeley 4, California



MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 15, NUMBER 8

OCTOBER, 1960

Contents

	PAGE
DISTRIBUTIONAL NOTES ON PLANTS OF THE WARM SPRINGS AREA, OREGON, <i>Robert Ornduff and David H. French</i>	225
G. THOMAS ROBBINS (1916-1960), <i>Rimo Bacigalupi</i>	231
STUDIES IN THE PERENNIAL GENTIANS: G. NEWBERRY AND G. TIOGANA, <i>Charles T. Mason</i>	233
CHROMOSOME COUNTS IN THE SECTION SIMIOLUS OF THE GENUS MIMULUS (SCROPHULARIACEAE). IV., <i>Barid B. Mukherjee and Robert K. Vickery, Jr.</i>	239
FLOWERING RESPONSES IN PHACELIA SERICEA AND P. IDAHOENSIS, <i>George W. Gillett</i>	245
REVIEWS: Roxana Stinchfield Ferris, <i>Illustrated Flora of the Pacific States. Washington, Oregon, and California. Volume IV — Bignoniaceae to Compositae</i> (Helen K. Sharsmith); Jens Clausen and W. M. Hiesey, <i>Experimental Studies on the Nature of Species. IV. Genetic Structure of Ecological Races</i> (Henry J. Thompson).	249
INDEX TO VOLUME XV	253

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$6.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

BOARD OF EDITORS

HERBERT L. MASON, University of California, Berkeley, Chairman

EDGAR ANDERSON, Missouri Botanical Garden, St. Louis

LYMAN BENSON, Pomona College, Claremont, California.

HERBERT F. COPELAND, Sacramento College, Sacramento, California.

JOHN F. DAVIDSON, University of Nebraska, Lincoln.

IVAN M. JOHNSTON, Arnold Arboretum, Jamaica Plain, Massachusetts.

MILDRED E. MATHIAS, University of California, Los Angeles 24.

MARION OWNBEY, State College of Washington, Pullman.

IRA L. WIGGINS, Stanford University, Stanford, California.

Secretary, Editorial Board—ANNETTA CARTER

Department of Botany, University of California, Berkeley.

Business Manager and Treasurer—JOHN H. THOMAS,

Dudley Herbarium, Stanford University, Stanford, California

CALIFORNIA BOTANICAL SOCIETY, INC.

President: Herbert G. Baker, Department of Botany, University of California, Berkeley, California. First Vice-president: Malcolm A. Nobs, Carnegie Institution of Washington, Stanford, California. Second Vice-president: Herbert F. Copeland, Sacramento City College, Sacramento, California. Recording Secretary: Mary L. Bowerman, Department of Botany, University of California, Berkeley, California. Corresponding Secretary: Francia Chisaki, Department of Botany, University of California, Berkeley, California. Treasurer: John Thomas, Dudley Herbarium, Stanford University, Stanford, California.

DISTRIBUTIONAL NOTES ON PLANTS OF
THE WARM SPRINGS AREA, OREGON

ROBERT ORNDUFF AND DAVID H. FRENCH

In an earlier paper (Ornduff and French, 1958) we reported a number of distributional novelties discovered during the course of identification of nearly 2000 vascular plant specimens from the Warm Springs Indian Reservation in Oregon. This collection of plants was made in connection with ethnobotanical studies of the Chinookan (French, 1956), Sahaptin, and Paiute Indians at Warm Springs. The reservation consists of approximately 564,000 acres located in the southwest portion of Wasco County and the northwestern portion of Jefferson County in north-central Oregon. The summit of the Cascade range forms the western limit of the reservation, the Metolius River most of the southern boundary, and the Deschutes River in the central Oregon plateau the eastern boundary. The northern reservation boundary has been the subject of recent litigation and is technically farther north than indicated on most maps and marked on Highway 26. Our references in this paper are to the latter point on the highway, which we understand is located about 6.5 miles south of the junction of Highway 26 with Highway 52 (in Township 6 South, Range 10 East, Section 11, Willamette Base Line and Meridian).

Few plants from higher altitudes are represented inasmuch as most of our collecting was confined to areas visited by Indians—the yellow pine forests, wooded valley bottoms, and the treeless sagebrush and bunchgrass region. About 600 species are known to occur on the reservation, of which at least 56 are introduced. Herein we record additional novelties of distribution beyond those recorded in our first paper. Previously accepted distributional ranges are taken from such sources as Abrams (1940–51), Peck (1941), and Hitchcock, Cronquist, Ownbey, and Thompson (1955–59). In some of these works the ranges of the species are often broadly phrased and risk being over-generous. We have decided to eliminate from our list most, but not all, of those species covered by broad or ambiguous statements. It should be noted that our own discussions do not necessarily cover the total ranges of the species; unless otherwise stated, the statement of range following each species refers only to its distribution within Oregon.

We have examined specimens deposited in the herbaria at the University of Oregon (ORE), Oregon State College (OSC), University of California, Berkeley (UC), Willamette University (WILLU), and the University of Washington (WTU). We extend our thanks to the staffs of these herbaria for their many courtesies during our visits.

Our study of herbarium specimens confirmed our impression that the Warm Springs Reservation has seldom been visited by collectors. In some instances, however, we found in the above herbaria specimens from the

Warm Springs area which alter the ranges of the species as they are now known through publication. The most significant of these collections are noted in our list.

Most of our specimens were identified by the first author, but the following specialists have also assisted: the late Carleton Ball (*Salix*), Francia Chisaki (*Boraginaceae*), Lincoln Constance (*Umbelliferae*), LeRoy Detling (*Cardamine*), Marion Ownbey (*Allium*), and the late Albert N. Stewart (*Panicum*). Arthur Cronquist and C. Leo Hitchcock have provided determinations in a large number of families. We are indebted to these botanists for their assistance.

In the following list the second author's collection numbers are used and, for the most part, the specimens exist as unicates in his herbarium at Reed College. Where noted, duplicates are at the New York Botanical Garden (NY) and the Herbarium of the University of California, Berkeley (UC). Because most of the collections were not made in duplicate and are thus not incorporated in larger herbaria, we feel justified in presenting these reports of new distributional data.

NATIVE SPECIES

PANICUM PACIFICUM Hitchc. & Chase. This grass is rarely collected in Oregon east of the Cascades. Our specimen, No. 908, is from beside the Warm Springs River near the Agency-Simnasho road, Wasco County, and differs little from the coastal *P. occidentalis* Scribn., which may not be distinct. Other relevant collections: *Peck 15781* (WILLU) from Maupin, Wasco County, and *Peck 17490* (WILLU) from Imnaha, Walwola County.

CAREX EURYCARPA Holm. Although frequently collected on the eastern slopes of the Cascades in Deschutes and Klamath counties, this sedge is rare to the northward in central Oregon. It has been collected from the east side of Mount Hood, Hood River County, *Henderson 959* (ORE); from the Suttle Lake area, Jefferson County, *Hitchcock & Martin 4883*; and our specimen, No. 1494 (NY) is from the east bank of the Deschutes River, near the Highway 26 bridge, Jefferson County.

ALLIUM MACRUM S. Wats. Published records limit this onion to the Blue Mountain region of Oregon and Washington, but the species appears to be well-distributed in our area. We collected it on Miller Flat, Jefferson County, No. 597, and on Sidwalter Flat, Wasco County, No. 1763—both near Highway 26. Other Wasco County collections: near Kent, *Baker 804* (OSC, WTU); near Shaniko, *Cronquist 6935* (OSC, WTU), *Gale 99* (WTU); eight miles south of Maupin, *Peck 26247* (WILLU).

ALLIUM NEVII S. Wats. According to Marion Ownbey (in litt.) this species is infrequently collected in Oregon. It grows north of the reservation in Wasco County (cf. *Peck 26216* (WILLU) and other collectors); we found it on Sidwalter Flat, Wasco County, No. 1811 (duplicate at Washington State University, Pullman).

ALLIUM TOLMIEI Baker. Recorded east and southeast of the reservation, this onion appears to be well-distributed in our region. Our collection is from one mile up Tenino Creek valley from the Agency, Jefferson County, Nos. 478*A*, 478*B*; also collected in this county by *Steward* 6379 (OSC, WTU), Madras.

SALIX DRUMMONDIANA Barratt var. *SUBCOERULEA* (Piper) Ball. In Oregon, this species is rarely collected. Peck (1941) lists it only from the Wallowa Mountains, but our specimens are from thickets above Shitike Creek, near the Agency, Jefferson County, Nos. 40, 1291*A*, 1291*B*; also collected in Deschutes County, *Whited* in 1907 (OSC) and Grant County, *Henderson* 5165 (ORE).

ATRIPLEX CONFERTIFOLIA (Torr.) S. Wats. A member of the Great Basin flora which is sparingly represented on the reservation, this species is known from a considerable distance east of Warm Springs in Wheeler County. It appears to reach its northwestern limit on the reservation, where it grows with *Sarcobatus vermiculatus* (Hook.) Torr. on an alkaline flat in Wolfe Hollow, No. 1287.

ACER CIRCINATUM Pursh. Though found mainly to the west of the Cascades, this maple is commoner on the eastern slopes than previously suspected. It is frequent near Beaver Creek (No. 353 came from the north boundary, Wasco County) and occurs along water courses traversing the more arid parts of the reservation. No. 205 was collected less than two miles west of the Agency, near Shitike Creek, Jefferson County. Other collections noted in herbaria are from scattered localities in Jefferson and Wasco counties. Warm Springs Indians say that they formerly obtained the tough wood locally and used it for fishing net hoops.

ANGELICA CANBYI Coult. & Rose. This species has not been reported from the Warm Springs region, where we have collected it south of Simnasho, Nos. 71 and 1966 (UC); Indian Head Canyon, No. 1273; near Beaver Creek bridge on the Simnasho-Hehe Butte road, Nos. 1279, 1423, 1917, 1954 (UC); and near Nena Creek, No. 1553—all in southern Wasco County. Other relevant specimens: *Thompson* 4951 (WTU), Tygh Hill, Wasco County; and *Peck* 18646, near summit, Ochoco Forest, Crook County.

LOMATIUM COUS (S. Wats.) Coult. & Rose. Apparently not previously collected as far west as Warm Springs, where it is locally abundant. *Peck* 26166 (WILLU), from eight miles south of Maupin, Wasco County, is near the reservation. Our Wasco County specimens: Nos. 473, 528, south side of Warm Springs River valley, near Agency-Simnasho road; Nos. 1219, 1869 (UC), Sidwalter Flat, near Highway 26. Jefferson County: No. 649, Miller Flat, north of Highway 26. Like other Indians of the Columbia Plateau, the Warm Springs Indians dig the starchy tubers for food.

LOMATIUM LEPTOCARPUM (Torr. & Gray) Coult. & Rose. Published records locate the western limit of this umbellifer in the Blue Mountains. However, *Cronquist* 7425 (UC) came from Big Summit Prairie, Wheeler

County, and Peck has collected the species in various parts of Wasco County. Our Nos. 526 and 1896 (UC) came from west of Simnasho, and Nos. 584A, 584B, 584C, and 1755 were collected about a mile northwest of Hehe Butte, all in Wasco County.

LOMATIUM NEVADENSE (S. Wats.) Coult. & Rose var. *NEVADENSE*. Warm Springs represents the northwestern limit for this Great Basin species, which was collected southeast of the Agency area longhouse, Jefferson County, Nos. 516A, 516B, 516C, and 1900 (UC).

PTERYXIA TEREBINTHINA (Hook.) Coult. & Rose var. *TEREBINTHINA*. Widely distributed in eastern Oregon, but not previously collected within many miles of Warm Springs. Both Nos. 1274 and 1897 (UC) came from Indian Head Canyon, near the Agency-Simnasho road, Wasco County; No. 1582 was collected from a rocky point north of the junction of the Whitewater and Metolius rivers, Jefferson County.

CAMPANULA SCOULERI Hook. Although frequent in the woods of western Oregon, this species is rarely reported east of the Cascades. There are a few northern Oregon collections from the region east of Santiam Pass and from the eastern slopes of Mount Hood. Our specimens were found near Highway 26 at the northern reservation boundary, Wasco County, No. 1342. Thus this species might be considered a regular inhabitant of the eastern slopes of the Cascades, at least in the northern portion of the state.

SENECIO MACOUNII Greene (= *S. fastigiatus* Nutt.) While this typically western Oregon species is very closely related to the eastern Oregon *Senecio canus* Hook., most specimens are clearly referable to one or the other species, and intermediates are lacking. A number of specimens from eastern Oregon have been referred by various collectors to *S. macounii*, although they more properly belong in *S. canus*. We have, however, found "good" *S. macounii* in the open pine woods at the Hehe celebration ground, Wasco County, Nos. 1463 and 1464 (both NY).

STYLOCLINE FILAGINEA Gray. Generally attributed to extreme eastern and southeastern Oregon, this species has recently been collected in Jefferson County 20 miles northeast of Madras, Peck 26156 (WILLU) and from a single colony in the Agency area at Warm Springs, our No. 1690 (NY).

TETRADYMIA GLABRATA Gray. Another species reaching its northwestern range limit on the reservation. In Oregon, it is most frequently collected in the southeastern counties, but recently it has been found near Mitchell, Wheeler County, Cronquist 7259 (OSC). Our plant, No. 1250 (NY), was growing southeast of Hehe Butte, Wasco County, about 75 miles northwest of Mitchell.

INTRODUCED SPECIES

RUBUS LACINIATUS Willd. Sparingly established in Shitike Creek valley west of the Agency, Jefferson County (No. 980). Only one other Oregon

specimen seen from east of the Cascade Mountains, *Small 30* (ORE), from Link River, Klamath County.

ANTHRISCUS SCANDICINA (Weber) Mansfield. This European species is well established in western Oregon, but only a single collection from east of the mountains was located in the herbaria: *Hitchcock 20441* (WTU), near the mouth of the John Day River, Sherman County. Our Nos. 827 and 942 came from a settled area west of the Agency.

MYOSOTIS MICRANTHA Pall. ex Lehm. In our earlier paper (Ornduff and French, 1958, p. 220) we mistakenly referred our No. 898 to *M. discolor* Pers. This has proved to be another Old World species, *M. micrantha*, as has our (previously uncited) No. 1808 from Sidwalter Flat, Wasco County.

DISCUSSION

In general, the new stations reported for the various species in the above list and in our previous paper are rather well-distributed over the reservation. There are few areas in which the "extra-limital" species are aggregated, as might be expected in view of both the geological and vegetational continuity of the reservation with much of the rest of central Oregon. An exception to this rule, however, is a large aggregation on or near the reservation of species characteristic of the more mesic western portions of the state, which are seldom collected east of the Cascade range. As might be expected, these species are typically inhabitants of moist ground along streams or rivers, or less frequently they are woodland plants. These species are: *Holcus lanatus* L., an introduction found in Wasco County by us and in Deschutes County by others; *Carex aperta* Boott., found by us in Wasco County, and known also from Union County; *Eleocharis obtusa* (Willd.) Schultes, known from Hood River, Umatilla, and Union counties, and here reported from Jefferson County; *Cardamine oligosperma* Nutt., found outside the reservation in Wasco County and Sherman County, as well as by us inside the reservation in Wasco County; *Perideridia oregana* (S. Wats.) Mathias, found by us in two localities on the reservation in Wasco County, and known also from various Klamath County collections; *Trichostema oblongum* Benth., infrequent in the counties south of the reservation and collected by us on the reservation in Wasco County; *Artemisia douglasiana* Bess., growing along the Deschutes River in Jefferson County; and *Gnaphalium chilense* Spreng., sporadic in Deschutes and Umatilla counties and found by us in Jefferson County as well.

In addition to these characteristically western species which are seldom collected east of the Cascades, we have noted additional species which have apparently never been reported from east of these mountains. These are: *Juncus effusus* L. var. *pacificus* Fern. & Weig., locally abundant along Shitike Creek, west of the Agency, Jefferson County, Nos. 215, 940, and 1509 (NY) as well as along Beaver Creek near the north reservation boundary, Wasco County, No. 1644; *Achlys triphylla* (Smith)

DC., found well down on the eastern slopes of the Cascades at the north reservation boundary near Highway 26, No. 363, and near the upper Warm Springs River, No. 866, both Wasco County; *Ribes sanguineum* Pursh, various collections noted from Jefferson County sites, and also found in a number of localities along upper Beaver Creek where it parallels Highway 26, e.g., our Nos. 355, 627A, 627B; *Angelica genuflexa* Nutt., found in scattered moist areas southeast of Mount Hood in Wasco County, as near Highway 26 one mile north of the north reservation boundary, No. 1846 (UC), and also collected by other workers east of the Cascade summit in Klamath County; *Gentiana sceptrum* Griseb., collected in a damp meadow near Highway 26 several miles southeast of its junction with Highway 52, Wasco County, No. 1389; and *Veronica serpyllifolia* L. var. *serpyllifolia* from along Beaver Creek about 0.5 miles northwest of the Highway 26 intersection with the north reservation boundary, Wasco County, No. 1803.

Most of the species discussed in the present and previous papers fall into two phytogeographical groups: (1) those which occur at Warm Springs in populations disjunct from the reported range of the species, and (2) those which appear to be beyond the margins of their previously reported ranges. In the first group are species such as *Convolvulus polymorphus*, *Phacelia thermalis*, and *Stylocline filaginea*. Intensive collecting in the areas adjacent to the reservation will likely show that many of these apparently disjunct stations are in fact connected with the main range of the species by geographically intermediate populations. In the second group are species such as *Pinus lambertiana*, *Allium macrum*, *Achlys triphylla*, *Angelica genuflexa*, and *Tetradymia glabrata*, many of which appear to be at their northern, southern, eastern, or western limits. The majority of the species in this latter group are those typical of the more mesic western portions of the state which have evidently migrated into suitable sites in our region either through the Columbia gorge and thence southward along the eastern slopes of the Cascades, or via the low mountain passes in the Cascades. Undoubtedly most of the weedy species reported are relatively recent introductions which may or may not become permanent members of the naturalized flora of the reservation. It is likely that a few native species, such as *Phacelia thermalis*, have been recently introduced and will not become established. However, the majority of the species we have discussed are well-established and occur in large colonies and/or in a number of widely separated vigorous populations. A notable exception is *Pinus lambertiana*, represented on the reservation by a few isolated senescent individuals which are not reproducing.

Department of Botany,
University of California, Berkeley.
Reed College,
Portland, Oregon.

LITERATURE CITED

- ABRAMS, LEROY. 1940-1951. *Illustrated Flora of the Pacific States*, vols. I-III. Stanford, California. Stanford University Press.
- FRENCH, DAVID. 1956. An Exploration of Wasco Ethnoscience. *Year Book of the American Philosophical Society*, pp. 224-226.
- HITCHCOCK, C. LEO, ARTHUR CRONQUIST, MARION OWNBEY, and J. W. THOMPSON. 1955-1959. *Vascular Plants of the Pacific Northwest*, vols. IV & V. Seattle, University of Washington Press.
- ORNDUFF, ROBERT, and DAVID FRENCH. 1958. Notable Plants of the Warm Springs Indian Reservation, Oregon. *Leafl. West. Bot.* 8(9):217-220.
- PECK, MORTON E. 1941. *A Manual of the Higher Plants of Oregon*. Portland, Binford and Mort.

G. THOMAS ROBBINS (1916-1960)



Early on the morning of February 11th, 1960, a few days after his forty-fourth birthday, G. Thomas Robbins, Herbarium Botanist in the Jepson Herbarium of the University of California Botany Department, died quietly in his sleep. The resultant sense of shock and loss among his botanical colleagues, especially those in Berkeley, was both deep and lasting.

Tom Robbins was born in San Francisco on February 6, 1916. While

he was still a boy, his family moved to Windsor in Sonoma County, California, and in the local schools and those in Santa Rosa, Tom received his elementary and high school education. His early interest in matters botanical was stimulated by the guiding hand of Mr. Milo S. Baker, who was his Professor of Botany during the two years of Tom's attendance at Santa Rosa Junior College. Later he attended the University of California at Berkeley, working meanwhile as a valuable student assistant in the University Herbarium, and graduating there in Botany in 1938 with a Bachelor of Arts degree. Later, he spent a profitable year at the University of Colorado during which he wrote an excellent monograph of the North American species of *Androsace*, which was later published in the American Midland Naturalist (Vol. 32, pp. 137-163, 1944). This work earned him the Master of Arts degree in 1941.

In 1946, Tom was appointed Associate Professor of Biology at the East Central State College at Ada, Oklahoma. Tom enjoyed his teaching activities greatly, but increasing deafness, which had been plaguing him for several years, became so acute as to force his retirement from a teaching career at the end of the school year in 1949.

Subsequently, for nearly three years, Tom was engaged as one of several botanical assistants aiding Dr. Herbert Mason, Director of the Herbarium of the University of California, in the preparation of "A Flora of the Marshes of California." Tom carried on some of the field work in connection with this project, contributed the final draft of the manuscripts of the Gramineae and Cyperaceae as well as of some genera in which he had a special interest, and aided in the solution of many taxonomic, bibliographic, and nomenclatural problems. Early in 1952, Tom joined the staff of the Jepson Herbarium as Herbarium Botanist, a position which he filled most capably, contributing manuscript on selected genera treated in the still unpublished portions of Jepson's "A Flora of California," which position he held at the time of his lamentably untimely death.

For some years, Tom gave unstintingly of his time and effort to fulfill the often thankless chores associated with his activities as Corresponding Secretary of the California Botanical Society.

As in the case of so many of his other pursuits, Tom's passion for excellence eventually resulted in his becoming a very fine photographer of close-up studies of native flowers, as the Kodachrome collection which he built up for the Jepson Herbarium well attests. Thus, as in his botanical endeavors, his life was enriched by a happy merging of vocational and avocational pursuits. Purely on the avocational level, Tom's interest in and understanding of music brought meaningful enjoyment, often shared with his closest friends, to his leisure hours.

Tom Robbins' outstanding characteristics were his gentleness, charity in judgment, an unusual ability to keep his own counsel, a passion for accuracy, and a tendency to reserve his judgment, either botanical or otherwise, until all pertinent data had been fully assessed and "digested."

To quote from a letter from Joseph Ewan, who was his professor while he attended the University of Colorado, "his meticulous care, almost fanatical, in the handling of records, and extreme interest in assembling all the pertinent literature on a topic before committing himself by way of a botanical judgment" were among his most valuable assets. These characteristics are amply exemplified in his last published work, "Notes on the Genus *Nemacladus*" (Aliso, Vol. 4, pp. 139-147, 1958), in which two new species and new interpretations of already published taxa were published.

Tom's name is commemorated in *Phacelia strictiflora* Gray var. *Robbinsii* Constance (Contr. Gray Herb. 168:20, 1949), which was based on one of Tom's collections in Oklahoma.

Besides his membership in the California Botanical Society, he was a member of Sigma Xi, the Society for the Study of Evolution, and of the International Association for Plant Taxonomy.

Tom Robbins will long be missed by those whose good fortune it was to know him at all well.—RIMO BACIGALUPI, Jepson Herbarium, Department of Botany, University of California, Berkeley.

STUDIES IN THE PERENNIAL GENTIANAS:

G. NEWBERRYI AND G. TIOGANA¹

CHARLES T. MASON, JR.

Gentiana newberryi Gray is the name applied to a group of dwarf perennial gentians of Section *Pneumonanthe*, which occurs in the Sierra Nevada and Cascade Mountains of California and Oregon. The name is used in many manuals (Abrams, 1951; Jepson, 1925; Munz, 1959; Peck, 1941) to embrace not a single species but two species and a number of intermediate forms. While the author was studying the western perennial gentians under a National Science Foundation grant, the problem came to light, and an attempt is here made to resolve the difficulty.

Asa Gray described *Gentiana newberryi* from material collected in Oregon by Newberry, a member of the Williamson Pacific Railroad expedition of 1855. He first presented the new name in a hand-written description on the type sheet in the Gray Herbarium. Only the Newberry specimen was cited with this description. However, by the time the name was published (Gray, 1876), the circumscription was modified to include California material, and a Bolander collection from Mariposa County was added as a syntype.

Three other names have been applied to this complex. In 1931 Eastwood described *G. copelandii*, which she separated from *G. newberryi* on the "much broader leaves and dark purple flowers." The name *G. copelandii*, having been used previously by Greene (1904) and by Elmer

¹Arizona Agricultural Experiment Station Technical Paper No. 568.

(1915), was invalid, causing Eastwood to correct the name of this species to *G. eximia* (Eastwood, 1934). A third species, *G. tiogana*, was recognized in 1940 by Heller, who separated it from *G. newberryi* by its smaller size.

Of the three validly published names, *G. newberryi*, *G. eximia*, and *G. tiogana*, only the first has been accepted by students of the flora of California and Oregon. The present author, after studying many field and herbarium specimens, is convinced that two species should be recognized. They are both perennials with a rosette of leaves and with flowering stalks arising from the axils of last year's leaves. Each flowering stalk usually has a single flower, and the patterning on the flowers is the same; however, the two species can be separated by the following characters:

- Flowers 4.0–5.5 cm. long; corolla bright blue with 5 dark greenish stripes, the lobes 1.0–1.5 cm. long; plicae many-lobed with two long thin central lobes 0.7–0.9 cm. long; leaves broadly spatulate to suborbicular . . . *G. newberryi*
 Flowers 2.5–3.5 cm. long; corolla white or very pale blue with 5 dark greenish-brown stripes, the lobes 0.7–0.8 cm. long; plicae 0.4 cm., two-lobed with an occasional third or fourth lobe; leaves lanceolate to narrowly obovate *G. tiogana*

GENTIANA NEWBERRYI Gray, Proc. Am. Acad. 11:84. 1876. *Pneumonanthe newberryi* (Gray) Greene, Leaf. Bot. Obs. 1:71. 1904. *Dasystephana newberryi* (Gray) Arth. Torrey 22:30. 1922. *Gentiana copelandii* Eastw. Proc. Calif. Acad. Sci. Series 4, 20:150. 1931; non *Gentiana copelandii* Greene, 1904, or Elmer, 1915. *Gentiana eximia* Eastw. Leaf. West. Bot. 1:96. 1934.

Low rhizomatous perennial with a rosette of broadly oblong-spatulate to suborbicular leaves up to 6 cm. long and 2 cm. wide; flowering stems 1–5, decumbent to erect, 15 cm. long, from axils of last year's leaves; flowers 4.0–5.5 cm. long and usually 1 per stem; calyx tube 0.8–1.5 cm. long, the lobes 0.7–1.1 cm. long, lanceolate to elliptical; corolla convolute in the bud, funnellform after anthesis, 4.0–5.5 cm. long, bright blue with 5 dark purple stripes extending from the tips of the lobes to the base of the corolla, the lobes 1–1.5 cm. long, entire or erose, broadly rounded with yellow-green dots on the inner surface and extending down into corolla tube, the apices apiculate; plicae 0.7–0.9 cm. long, bifid with two long attenuate lobes and several secondary lateral projections; stamens maturing before the pistil, the anthers extrorse; style none; capsule ellipsoidal, 1.5 cm. long, the stipe 1.5 cm. long; seeds broadly winged all around.

Type. Crater Pass, west side Cascade Mountains, lat. 44°, Oregon, *Newberry* s.n. (GH). Type was seen.

Gentiana newberryi is known only from the Three Sisters in the Cascade mountain area of central Oregon, and from the Mount Eddy region in Siskiyou and Trinity counties, California. An unexplained distributional gap exists from northern California to central Oregon. A similar disjunct distribution is exhibited by *Limnanthes douglasii* R. Br.

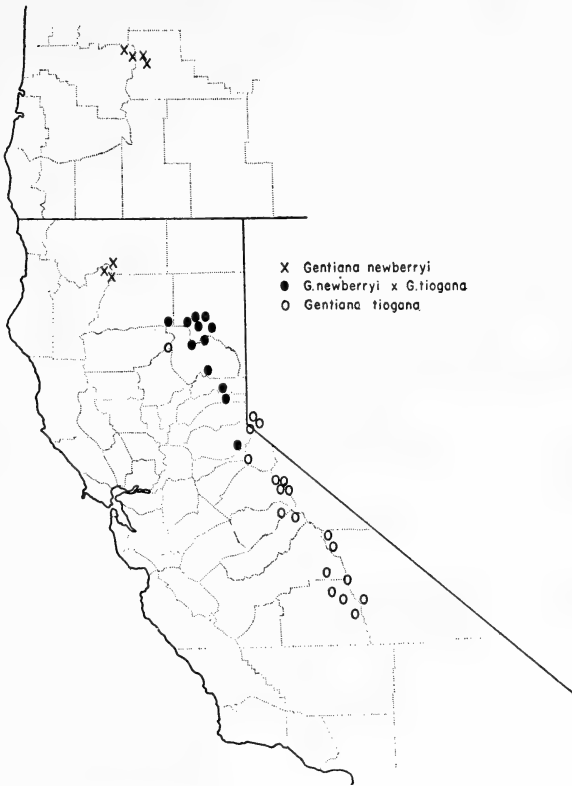


FIG. 1. Distribution of *Gentiana newberryi*, *G. tiogana*, and their hybrid in Oregon, California, and Nevada.

var. *douglasii*, which has the northern limit of its California distribution in Humboldt County and is again found in the Umpqua Valley, Douglas County, Oregon (Mason, 1952).

Representative specimens. OREGON. Deschutes County: Three Creeks Meadow, *Brandt & Steward* 6985 (ID, UTC), *Ellis & C. Mason* 1712; meadow near Three Creeks Lake, *Whited* 478 (WS), *Ellis & C. Mason* 1711; Fremont's Crossing of Tumalo Creek, *Whited* 479a (WS). Lane County: 5 miles west of McKenzie Pass, *Campbell* 17497 (CAS); Hand Lake, 4 miles west of Lane-Deschutes county line, *T. & C. Mason* 1791.

CALIFORNIA. Siskiyou County: Mount Eddy, *Copeland* 3878 (CAS), *Eastwood* 2037 (type of *G. copelandii* Eastw., CAS.). Trinity County: Morris Meadow, *Stuart Fork*, *Alexander & Kellogg* 5525 (UC); edge of Bull Lake, *Parker* in 1947 (DS).

GENTIANA TIOGANA Heller emend. C. T. Mason. *G. tiogana* Heller, *Leaf. West. Bot.* 2:221-222. 1940.

Low rhizomatous perennial with a rosette of obovate to spatulate leaves ca. 4 cm. long and 1 cm. wide; flowering stems 1 or 2, decumbent to erect, 5-7 cm. long, from the axils of last year's leaves; flowers 2.5-3.5

cm. long, usually 1 per stem; calyx tube 0.6–1.0 cm. long, the lobes 0.6–1.0 cm. long, lanceolate to elliptical; corolla convolute in the bud, funnel-form after anthesis, 2.5–3.5 cm. long, white or very light blue with 5 greenish-brown stripes extending from the tips of the lobes to the base of the corolla, the lobes 0.7–0.8 cm. long, entire or erose, narrow with yellow-green dots on the inner surface and extending down into corolla tube, the apices apiculate; plicae 0.4 cm., with 2 large lobes and an occasional third or fourth smaller lateral lobe; stamens maturing before the pistil, the anthers extrorse; capsule ellipsoidal, 1.0–1.2 cm. long, the stipe 1.0 cm. long; seeds broadly winged all around.

Type. Shore of a lakelet outside Yosemite National Park, Tioga Pass, Mono County, California, *Heller 15453* (WTU #79272. Isotypes, CAS, DS, NY, UC, WTU). The type specimen was not seen, but the information was transmitted by letter from C. L. Hitchcock. Isotypes from California Academy of Sciences, Dudley Herbarium, and University of California were seen.

Heller's labels agree on the collection number, the date, and that the collection was made outside Yosemite Park boundary. They vary to some degree on the other data presented. The county is listed as either Mariposa or Mono. As the park boundary is also the county line, "outside the park" would be Mono County. The distance outside the park varies from a few yards to one-fourth mile, and the elevation ranges from 9900 to 9940 feet. The labels also state, "south of Tioga Pass entrance"; the park boundary at that particular point extends east and west so that south of the entrance would be inside, not outside, the park. Heller probably considered the general direction of travel from Mono Lake to the Tioga Pass entrance through Leevining Canyon as west; therefore, to the left would be south. In the area to the east of the road at the Tioga Pass entrance is a meadow with a number of lakelets, and it undoubtedly is in this area that Heller made his collection.

The specific epithet *tiogana* was applied by Heller to specimens which, because of their smaller size, he considered distinct from the Sierra Nevada material recognized as *Gentiana newberryi*. This small form has been collected several times from the higher elevations and may warrant varietal recognition, but this author does not consider it distinct enough to be separated as a species; consequently Heller's epithet becomes the first applied to this group and must be used, and his description has been here emended to include the larger forms.

Representative specimens. CALIFORNIA. Inyo County: Big Pines Lake, *Howell 24123* (CAS); Mosquito Flat, Rock Creek, *Halperin 605* (CAS), *Ferris & Lorraine 11086* (DS); Heart Lake, Rock Creek Basin, *Peirson* in 1933 (DS, UC), *Peirson 9483* (COLO); Kearsarge Pass Trail west of Independence, *Alexander & Kellogg 3291* (DS, UC); Brown Lake, *Raven & Stebbins 254* (CAS, UC); Cottonwood Lakes, *Alexander & Kellogg 3316* (DS, UC, UTC). Tulare County: Crabtree Meadows, *H. M. & G. Hall 8442* (UC); Lost Canyon, *Howell 17787* (CAS); Rock Creek, *Howell 25515* (CAS, UC, UTC, WS); Army Pass, *Howell 26045* (CAS); Sequoia-Mount Whitney trail, *Sisson & Kobs* in 1928 (COLO); Humphrey Basin, *Moran 490* (DS). Fresno County: Hilgard Branch, Bear Creek, *Raven 7872* (CAS);

Humphrey Basin west of Mount Humphreys, *C. Sharsmith* 3149 (UC). Madera County: Iron Creek, *Raven* 3809 (CAS). Mariposa County: Mount Hoffman, *Rodin* 885 (UC). Mono County: Slate Creek, Hall Natural Area, *Clausen* 920 (DS, UC), *C. Mason* 1514; Dana Meadow, Tioga Pass, *Rowntree* in 1931 (CAS); $\frac{1}{2}$ mile upstream from Camp Tioga along Slate Creek, *C. Mason* 1512; southwest end Little Virginia Lake, *Hendrix* 604 (UC); Soda Springs, Tuolumne Meadows, *Eastwood* 625 (CAS); Bourland Meadows, *Belshaw* 81 (UC); Dana Plateau, northwest of Mount Dana, *C. Sharsmith* 2331 (UC); White Mountain, Mount Conness Range, *H. Mason* 11339 (UC); Ten Lakes Basin, *H. Sharsmith* 1329 (UC); near Dog Lake, *Howell* 20434 (CAS). Alpine County: meadow 3 miles west of Lake Alpine, *C. Mason* 1610. Eldorado County: Benwood Meadows, Camp Echo, *Heller* 12264 (CAS, COLO, DS, UC); Dicks Lake, Lake Tahoe, *Alexander & Kellogg* 3508 (UC); Meyers Station, *Clemens* in 1920 (CAS). Butte County: Jonesville, Spring Creek, *Copeland* in 1931 (UC). NEVADA. Washoe County: 3 miles south Mount Rose, *Hitchcock & Martin* 5542 (DS, UC, UTC, WS); Galena Creek, south base Mount Rose, *Hitchcock & Martin* 5522 (DS, UC, UTC); Mount Rose, *Heller* 9970 (CAS, DS, MONTU).

Naturally and artificially produced hybrids among the gentians are well-known (Mason, 1959), and a number of herbarium specimens from northern California show evidence of hybridization and introgression between *G. tiogana* and *G. newberryi*. Three collections from Eldorado County (Wrights Lake, *Johannsen* 452, UC; $\frac{1}{2}$ mile north of Wrights Lake, *Robbins* 1355, CAS, UC; and Echo Summit, *Howell* 22974, CAS) have the characteristics of *G. tiogana* except that the plicae tend to be long and narrow.

Several collections from Nevada, Sierra, Plumas, Lassen, and Shasta counties in California have characteristics of both species. Specimens from Sage Hen Creek (*H. Mason* 14472, UC), and Independence Lake (*Floyd* in 1925, CAS, *Alexander & Kellogg* 5160, UC), of Nevada County, and Webber Lake, Sierra County (*Dudley* in 1894, DS) have stem length, leaf size but not shape, and plicae lobing which approach those of *Gentiana newberryi*. The flower size is intermediate, ranging from 3.5–4.3 cm. on the collections from Independence Lake, and 3.8–4 cm. on the other two collections. The plicae are of the larger type found in *G. tiogana*, and the green and white flower color of that species is specified on Mason's collection. Possibly the larger size of the leaves and stems is the result of ecological rather than genetic factors.

A sheet of specimens from Mount Elwell, Plumas County (*Wicks* 2889, UC), has flowers and leaves approaching those of *G. newberryi*. The flowers are 4–4.5 cm. long and the calyx lobes are large and elliptic. The plicae, although multilobed, are the large type of *G. tiogana*. The flower color is not specified, but the specimens appear dark as though there may be some blue factors present. One plant on the sheet is quite different from the others; it has the smaller flowers, smaller leaves, white color, and heavy plicae of *G. tiogana*. The presence of the two types in the same collection gives good evidence that both are present in the same area so that hybridization might occur between the two species.

Several collections from northern Plumas County (Big Meadows, *Coombs* in 1912, CAS, UC, *Austin* 399, UC; Prattville, *Coombs* in 1906, CAS), southeastern Shasta County (Lassen's Peak, *Brewer* 2175, UC;

upper King's Creek Meadow, *Hoover 4612*, UC), and southwestern Lassen County (Susanville, *Safford s.n.*, UC; Mountain Meadows, *Austin* in 1879, UC; Hog Flat, *Stebbins et al 3998*, UC; Harvey Valley Spring, *Whitney 1505*, UC; a mile east of Westwood, *Heller 15341*, DS, UC) show evidence of introgression. Of particular interest are the two collections from Big Meadow which have several flowers per stem. This multiple flower condition is uncommon in either of these parent species, but it is seen on some collections by Lemmon which are affixed to the type sheet of *G. newberryi*. Undoubtedly these Lemmon collections were made from this northern California area, although the data on the label are vague and incomplete. The Brewer collection from Mount Lassen and Safford's collection from Susanville have very small plants and flowers and show more of the characters of *G. tiogana* than *G. newberryi*.

The two species under consideration are usually separated by altitudinal differences. Most collections of *G. newberryi* have come from areas between 4000 and 6500 feet in elevation, but one specimen from Bull Lake, Trinity County, California (*Parker* in 1947, DS) is listed as 7380 feet. *Gentiana tiogana* frequently is found above timberline, and specimens from 12,000–13,000 feet are not uncommon. The lowest elevation noted for a collection of *G. tiogana* is 7160 feet at Jackass Meadow, Fresno County (*Pearson 12880*, CAS).

The specimens cited as having characteristics of both species have been collected from areas which, for the most part, are intermediate in elevation between the usual requirements of the two parents. The collection of specimens from "a mile east of Westwood," *Heller 15341*, is cited as elevation 5000 feet, and these plants are predominantly of the *G. newberryi* type. On the other hand the collection from Lassen's Peak, *Brewer 2175*, was made at 8000 feet, and these specimens have the majority of their characters similar to *G. tiogana*. This overlap in the altitudinal distribution of intermediate forms might also be regarded as evidence that *G. newberryi* and *G. tiogana* hybridize in northern California.

Department of Botany
University of Arizona, Tucson

LITERATURE CITED

- ABRAMS, L. 1951. Illustrated flora of the Pacific States Vol. 3. Stanford Univ. Press.
ARTHUR, J. C. 1922. Changes in phanerogamic names. *Torreyia* 22:30.
EASTWOOD, A. 1931. New species of plants from western North America. *Proc. Calif. Acad. Sci. Ser. 4*, 20:150.
———. 1934. *Gentiana copelandii* Eastwood. *Leafl. West. Bot.* 1:96.
ELMER, A. D. E. 1915. Two hundred twenty-six new species. *Leafl. Philip. Bot.* 7:2671 (not seen).
GRAY, A. 1876. Miscellaneous botanical contributions. *Proc. Am. Acad. Sci.* 11:84.
GREENE, E. L. 1904. North American species of *Amarella*. *Leafl. Bot. Obs.* 1:53.
———. 1904. The genus *Pneumonanthe*. *Leafl. Bot. Obs.* 1:71.
HELLER, A. A. 1940. California plants, mostly new. *Leafl. West. Bot.* 2:221.
JEPSON, W. L. 1925. Manual of the flowering plants of California. Assoc. Students, Berkeley.

- MASON, C. T. 1952. A systematic study of the genus *Limnanthes*. Univ. Calif. Publ. Bot. 25:455-512.
- . 1959. A hybrid among the perennial gentians. *Brittonia* 10:40-43.
- MUNZ, P. A. 1959. A California flora. Univ. Calif. Press, Berkeley.
- PECK, M. E. 1941. A manual of the higher plants of Oregon. Binford and Mort, Portland.

CHROMOSOME COUNTS IN THE SECTION
SIMIOLUS OF THE GENUS MIMULUS
(SCROPHULARIACEAE). IV.

BARID B. MUKHERJEE AND ROBERT K. VICKERY, JR.

This report¹ on the determination of chromosome numbers in the section *Simiolus* of the genus *Mimulus* is part of a long range investigation into the evolution of species in *Mimulus* (Vickery, 1951). The chromosome numbers and configurations presented in this article indicate a lack of cytological differentiation between several of the currently accepted species (Pennell, 1951) of the section *Simiolus*. Also they reveal the presence of aneuploidy in different populations of two other species, and, lastly, they fill an important gap in the previously indicated (Mukherjee and Vickery, 1959) polyploid series that extends from North to South America.

Essentially the same method of bud fixation was employed as in the previous investigation (Mukherjee and Vickery, 1959), i.e., fixation in two parts absolute ethanol to one part glacial acetic acid saturated with ferric acetate, followed by staining of the anthers in iron-aceto-carmin. Work now in progress indicates that there may be possible improvements in this schedule. Each chromosome number determination is based on counts from an average of approximately eight pollen mother cells. Camera lucida drawings were made for three or four figures for each count and, in addition, photomicrographs were taken of many of the configurations. Herbarium specimens of each culture have been or will be deposited in the Garrett Herbarium of the University of Utah (UT).

¹ This work was supported by the National Science Foundation. Part of it was included in the dissertation of the senior author submitted to the Faculty of the University of Utah in partial fulfillment of the requirements for the Ph.D. degree.

The authors wish to thank the following people who made this study possible by so kindly gathering seeds or living plants for them: Lawrence Beane, Martin Brown, Annetta Carter, Norman V. Chamberlain, Jens Clausen, John L. Creech of the Plant Introduction and Exploration Division of the United States Department of Agriculture, William M. Hiesey, Richard W. Holm, Carl L. and Laura C. Hubbs, David D. Keck, Oliver Norwell, George T. Oberlander, the late Francis W. Pennell, Carl W. Sharsmith, G. Ledyard Stebbins, Jr., H. J. Venema, Delbert Wiens, and Ira L. Wiggins.

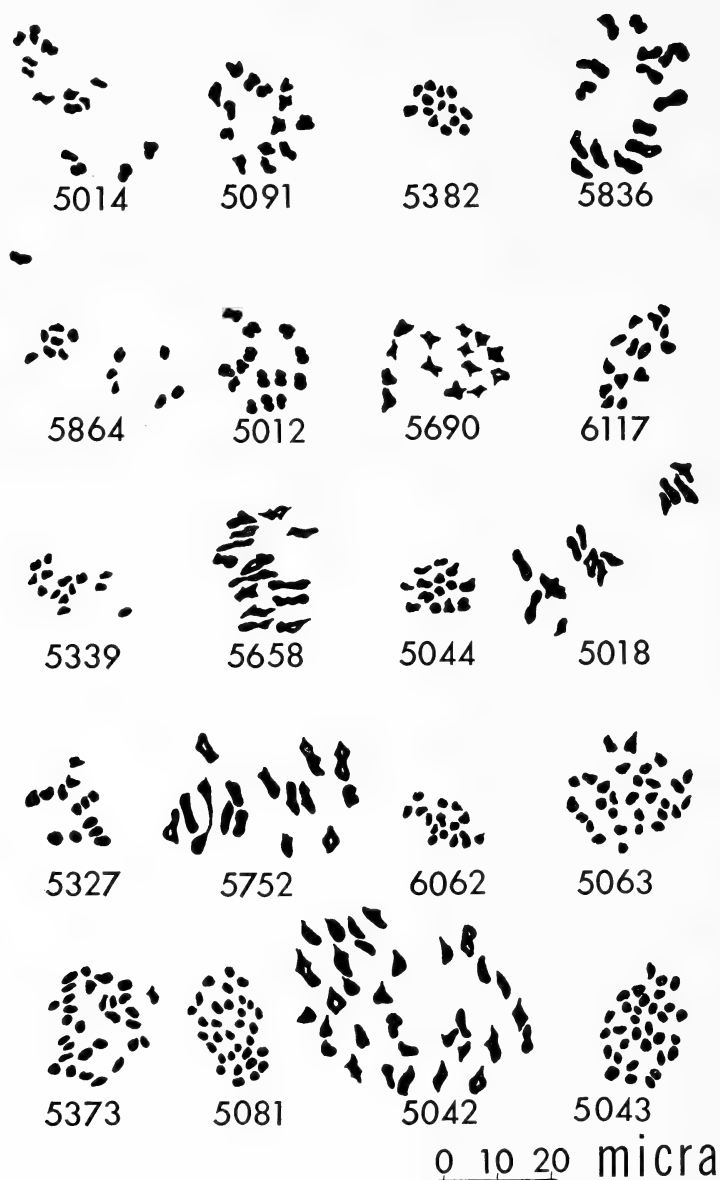


FIG. 1. Meiotic chromosomes of *Mimulus*: *M. guttaeus*, 5014, 5091, 5382, 5836, 5864; *M. tilingii* var. *tilingii*, 5012, 5690, 6117; *M. laciniatus*, 5339; *M. laxus*, 5658; *M. nasutus*, 5044, 5018, 5327; *M. platycalyx*, 5752; *M. glabratus* var. *utahensis*, 6062; *M. glabratus* var. *fremontii*, 5063, 5373; *M. tigrinus*, 5081; *M. luteus*, 5042, 5043. All cells are in or near second metaphase except 5382, 5836, 5012, 5690, 5658, 5018, and 5752, which are in first metaphase. (Camera lucida drawings as reproduced, = $\times 840$).

A total of thirty-three cultures was studied during the present investigation (see table 1). They include representatives of ten species and varieties of the section *Simiolus*: *Mimulus guttatus* DC., *M. tilingii* Regel var. *tilingii*, *M. laciniatus* Gray, *M. nasutus* Greene, *M. laxis* Pennell, *M. platycalyx* Pennell, *M. glabratus* var. *utahensis* Pennell, *M. glabratus* var. *fremontii* (Benth.) Grant, *M. tigrinus* hort., and *M. luteus* L.

All fifteen cultures of *M. guttatus* were found to have $n=14$ chromosomes. The configurations were regular and similar to those previously observed for other cultures of *M. guttatus* (Vickery, 1955; Mukherjee, Wiens, and Vickery, 1957; Mukherjee and Vickery, 1959) and, therefore, only a few of the camera lucida drawings of *M. guttatus* chromosomes were included in figure 1. The fifteen cultures examined represent much of the geographical range of *M. guttatus* (see table 1) and much of its morphological and physiological diversity as well. Morphologically the cultures differ from each other in the average height of the plants, shape of the leaves, amount and distribution of anthocyanin pigmentation, and in the size of the flowers. Physiologically they differ in growth rates, time and speed of flowering, and time and speed of maturing seeds. Cytologically the only detectable difference observed among the fifteen cultures was the presence of marked chromosome stickiness under the present fixation schedule in two of the annual races. Despite the wide range of morphological and physiological differences between the various cultures, they all exhibit apparently similar karyotypes.

The chromosome numbers of six cultures of *M. tilingii* var. *tilingii* from the Sierra Nevada (see table 1) were found to be $n=14$ as in *M. guttatus*. *Mimulus tilingii* var. *tilingii* is related to *M. guttatus* on the basis of morphology (Hitchcock, Cronquist, Ownbey and Thompson, 1959), but is separated from it by strong crossing barriers (Vickery, 1956). The chromosome configurations of the six cultures were regular and similar to those of *M. guttatus* and to our first *M. tilingii* var. *tilingii* count (Vickery, 1955), but differed in number from our more recent report of $n=15$ for a Utah population of *M. tilingii* var. *tilingii* (Mukherjee and Vickery, 1959). The populations studied represent much of the morphological diversity present in *M. tilingii* var. *tilingii* in the Sierra Nevada (table 1).

Mimulus laciniatus and *M. laxis*, species that are genetically closely related to *M. guttatus* (Vickery, 1956, and unpublished), were found to have $n=14$ chromosomes as does *M. guttatus*. The karyotypes of the three species are apparently indistinguishable. *Mimulus laciniatus* is morphologically strikingly different from *M. guttatus*, whereas *M. laxis* is closely similar. Probably *M. laciniatus* should be treated as a variety of *M. guttatus*, while *M. laxis* should be considered as synonymous with *M. guttatus*.

The chromosomes of three cultures from widely scattered populations (see table 1) of *M. nasutus* were counted. Two of the cultures have $n=13$ chromosomes and the third has $n=14$, which confirms the previous de-

TABLE 1. CHROMOSOME COUNTS IN *MIMULUS*, SECTION *SIMIOLUS*

- $n=14$ *M. guttatus* DC.
 Barry Summit, Humboldt County, California, altitude 3,400 feet, *Keck* 6007 (5005).
 Yosemite Junction (rocky creek), Tuolumne County, California, altitude 1300 feet, *Hiesey* 560 (5006).
 Lee Vining Canyon, Mono County, California, altitude 8000 feet, *Clausen* 2039 (5014).
 Kern River, Kern County, California, altitude 1000 feet, *L. Bean*, April 16, 1949 (5085).
 Botanic Garden strain, Hortus Cluj, Romania (5091).
 Rio Santo Thomas, Baja California, Mexico, altitude ca. 20 feet, *C. and L. Hubbs*, spring 1950 (5382).
 San Dimas Canyon, Los Angeles County, California, altitude 1500 feet, *R. K. Vickery, Jr.*, September 29, 1950 (5678).
 Hugh's Canyon, Salt Lake County, Utah, altitude 6000 feet, *N. Chamberlain*, spring, 1952 (5836).
 Skagg's Springs, Sonoma County, California, altitude ca. 50 feet, *R. Holm*, spring, 1951 (5864).
 Old Mine, Big Cottonwood Canyon, Salt Lake County, Utah, altitude 7650 feet, *Vickery* 683 (5961).
 Neff Canyon, Salt Lake County, Utah, altitude 5500 feet, *D. Wiens*, September 6, 1956 (5995).
 Moab, Grand County, Utah, altitude 4100 feet, *Vickery* 762 (6080).
 Cane's Spring, San Juan County, Utah, altitude 5800 feet, *Vickery* 763 (6081).
 Ledgemere, Big Cottonwood Canyon, Salt Lake County, Utah, altitude 5100 feet, *Vickery* 880 (6082).
 East Creek, Morgan County, Utah, altitude 5700 feet, *Vickery* 883 (6083).
- $n=14$ *M. tilingii* Regel var. *tilingii*
 Slate Creek (near Carnegie Transplant Garden), Mono County, California, altitude 10,000 feet, *Clausen* 2075 (5012). (In flower at time 6120, 6121, 6122 were collected in bud.)
 Budd Lake, Tuolumne County, California, altitude 10,250 feet, *C. W. Sharsmith*, September 13, 1950 (5690).
 Tributary to Slate Creek (near Carnegie Transplant Garden), Mono County, California, altitude 10,050 feet, *Vickery* 1379 (6117).
 Slate Creek (near Carnegie Transplant Garden), Mono County, California, altitude 10,000 feet, *Vickery* 1382 (6120). (Light green, large leaves.)
 Same locality—*Vickery* 1383 (6121), dark green, medium sized leaves.
 Same locality—*Vickery* 1384 (6122), dark green, small leaves.
- $n=14$ *M. laciniatus* Gray
 Lake Eleanor road, Tuolumne County, California, altitude 4200 feet, *Vickery* 179 (5339).
- $n=14$ *M. laxus* Pennell
 Yreka, Siskiyou County, California, altitude 3000–3200 feet, *Pennell* 26163 (5658).
- $n=14$ *M. nasutus* Greene
 Hasting's Reservation, Monterey County, California, altitude 1500 feet, *Stebbins* 701 (5044).
- $n=13$ *M. nasutus* Greene
 San Augustine Pass, Dona Ana County, New Mexico, altitude 4500 feet, *O. Norwell*, October 30, 1946 (5018).
 Wild Cat Creek, near Yosemite Junction, Tuolumne County, California, altitude 475 feet, *Vickery* 168 (5327).

-
- n=15 *M. platycalyx* Pennell
Crystal Lakes Reservoir, San Mateo County, California, altitude 800 feet,
G. Oberlander, April, 1951 (5752).
- n=15 *M. glabratus* var. *utahensis* Pennell
Johnson Pass, Tooele County, Utah, altitude 5800 feet, D. Wiens, October,
1956 (6062).
- n=30 *M. glabratus* var. *fremontii* (Benth.) Grant
Whipple Mountains, San Bernardino County, California, collected April 21,
1940. U.C. 667,449 (5063).
Kakernot Springs, Alpine Creek, Brewster County, Texas, Cory 53186, May 18,
1946 (5373).
- n=32 *M. tigrinus* hort.
Garden seed from the "Carlos Thays" Botanic Garden, Buenos Aires, Argentina
(5081).
- n=32 *M. luteus* L.
Vicinity of Illapel, Coquimbo, Chile, altitude 6200 feet, *Plant Introduction and
Exploration Division (U.S.D.A.) no. 144,535* (5042).
- n=30+0, 1, or 2 *M. luteus* L.
Vicinity of Illapel, Coquimbo, Chile, altitude 2000 feet, *Plant Introduction and
Exploration Division (U.S.D.A.) no. 144,536* (5043).
-

termination by G. L. Stebbins, Jr. (personal communication) for the same culture. The n=13 cultures exhibit partial crossing barriers with *M. guttatus*, whereas the n=14 culture crosses readily with *M. guttatus* (Vickery, 1956, unpublished). The cytologic and crossing results suggest to us that *M. nasutus* as presently described (Grant, 1924, and Pennell, 1951) includes at least two different entities. The proper naming of these entities must await further investigation and a detailed study of the taxonomic literature and type specimens of *M. nasutus* and its relatives.

Culture 5752, which was found to have n=15 chromosomes, was identified as *M. platycalyx* with some misgivings. Although the plants clearly exhibit Pennell's main key character of "fruiting calyces being fully as wide as long," yet the corolla throats are open and not filled by "a palate nearly closing orifice" (Pennell, 1951). Furthermore, Pennell had described *M. platycalyx* as occurring in the "southern Sierra Nevada from Mariposa to Tulare County, California," whereas the plants from which culture 5752 were grown came from the Crystal Lakes region of the outer Coast Ranges of California. However, even if this culture does not properly belong to *M. platycalyx*, it does represent an entity that is distinct from *M. guttatus* on the basis of morphology, crossing behavior (Vickery, 1956, in press), and cytology. Here again a sound taxonomic decision must await further critical study of this entity and the literature.

The culture of *M. glabratus* var. *utahensis* (6062) from the Stansbury Mountains near the Great Salt Lake had n=15 chromosomes as did culture 5265 from the population at Bicknell, Wayne County, Utah (Mukherjee, Wiens, and Vickery, 1957). In contrast, the population from the shore of Mono Lake at the western edge of the Great Basin has n=14 chromosomes (Vickery, 1955). Perhaps *M. glabratus* var. *utahensis* also

consists of two morphologically similar but cytologically different entities as does *M. nasutus*, although corroborative crossing data is not yet available.

Two cultures of *M. glabratus* var. *fremontii* from southern California and Texas were found to have $n=30$ chromosomes, although some of the plants of culture 5063 were observed to have as few as $n=26$ chromosomes. This chromosome number fills an important gap in the polyploid series connecting the Great Basin form, *M. glabratus* var. *utahensis*, $n=14$ and $n=15$, with the South American *M. glabratus* var. *parviflorus* (Lindl.) Grant, $n=45$, and its ally *M. pilosiusculus* HBK., $n=46$ (Mukherjee and Vickery, 1959). *Mimulus glabratus* var. *fremontii* is approximately intermediate in appearance between the other two varieties. It is 5 to 15 centimeters in height, whereas *M. glabratus* var. *utahensis* varies from 10 to 50 centimeters, and *M. glabratus* var. *parviflorus* is nearly prostrate. The leaves and flowers of *M. glabratus* var. *fremontii* are smaller than those of *M. glabratus* var. *utahensis* but larger than those of *M. glabratus* var. *parviflorus*. A broader cytogenetic and taxonomic study of the *Mimulus glabratus* complex of species is now being undertaken.

The culture of *M. tigrinus* from the Botanic Garden of Buenos Aires, Argentina, was found to have $n=32$ chromosomes. This count agrees with the previous reports of Brozek (1932), Sugiura (Darlington and Wylie, 1955) and the authors (1959).

Chromosome counts obtained for two different cultures of *M. luteus* tend to support the previously indicated relationship of the horticultural species, *M. tigrinus*, to this wild species (Mukherjee and Vickery, 1959). Culture 5042 has $n=32$ chromosomes on the basis of two plants studied whereas culture 5043 was variable on the basis of the five or six plants examined. Of the twenty-three cells studied eleven had $n=30$ chromosomes, six had $n=31$ and six had $n=32$. The cause of the variability was not clear from the data obtained. Perhaps accessory chromosomes are involved. Tentatively, the chromosome number for this culture appears to be $n=30+0, 1$ or 2 . The two cultures of *M. luteus* are morphologically similar, but are distinguishable on the basis of flower markings and the general growth habits of the plants.

In conclusion, this survey of chromosome numbers in section *Simiolus* has verified previously published counts for *M. guttatus* ($n=14$), *M. tilingii* var. *tilingii* ($n=14$), *M. glabratus* var. *utahensis* ($n=15$) and *M. tigrinus* ($n=32$). It has shown that two species that are genetically closely related to *M. guttatus*, *M. laciniatus* and *M. laxus*, have $n=14$ chromosomes also. In contrast, the culture, tentatively assigned to *M. platycalyx*, which is morphologically closely related to *M. guttatus* but genetically partially separated from it, has $n=15$ chromosomes. *Mimulus nasutus* appears to consist of two entities, one with $n=14$ chromosomes that is genetically closely related to *M. guttatus*, and the other with $n=13$ chromosomes that is genetically partially isolated from *M. guttatus* and from the $n=14$ form of *M. nasutus*. *Mimulus glabratus* var. *fremontii*

was found to have $n=30$ chromosomes, which neatly fills an important gap in the polyploid series of *M. glabratus* var. *utahensis*, $n=15$, to *M. glabratus* var. *parviflorus*, $n=45$. Lastly, one race of South American *M. luteus* has $n=32$ chromosomes, as had been previously reported for its horticultural derivatives, but the other race apparently has $n=30+0$, 1, or 2.

Department of Genetics and Cytology
University of Utah, Salt Lake City

LITERATURE CITED

- BROZEK, A. 1932. Mendelian analysis of the "red-orange-yellow" group of flower colors in *Mimulus cardinalis* Hort. *Preslia* 11:1-10.
- DARLINGTON, C. D. and A. P. WYLIE. 1955. Chromosome atlas of flowering plants. Allen and Unwin Ltd. London. 519 pp.
- GRANT, A. L. 1924. A monograph of the genus *Mimulus*. Ann. Missouri Bot. Gard. 11:99-388.
- HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY and J. W. THOMPSON. 1959. Vascular plants of the Pacific Northwest. Univ. Wash. Press, Seattle. 516 pp.
- MUKHERJEE, B. B. and R. K. VICKERY, JR. 1959. Chromosome counts in section Simiolus of the genus *Mimulus* (Scrophulariaceae). III. *Madroño* 15:57-62.
- MUKHERJEE, B. B., D. WIENS, and R. K. VICKERY, JR. 1957. Chromosome counts in Section Simiolus of the genus *Mimulus* (Scrophulariaceae). II. *Madroño* 14:128-131.
- PENNELL, F. W. 1947. Some hitherto undescribed Scrophulariaceae of the Pacific States. *Proc. Acad. Phila.* 99:155-199.
- . 1951. In *Illustrated Flora of the Pacific States* by LeRoy Abrams. Stanford Univ. Press. Vol. III, pp. 688-731.
- VICKERY, R. K., JR. 1951. Genetic difference between races and species of *Mimulus*. *Carnegie Institution of Washington Year Book* 50:118-119.
- . 1955. Chromosome counts in section Simiolus of the genus *Mimulus* (Scrophulariaceae). *Madroño* 13:107-110.
- . 1956. Data on interracial and interspecific hybridization in the section Simiolus of the genus *Mimulus* (Scrophulariaceae). *Utah Acad. Proc.* 32:45-64.
- . 1959. Barriers to gene exchange between the species of the *Mimulus guttatus* complex. *Evolution* 13:300-310.

FLOWERING RESPONSES IN PHACELIA SERICEA AND *P. IDAHOENSIS*¹

GEORGE W. GILLET

In the study of variation in the *Phacelia sericea* complex [*P. sericea* (Graham) A. Gray subsp. *sericea*; *P. idahoensis* Henderson; and intermediates], experimental cultures of *P. sericea* subsp. *sericea* and of *P. idahoensis* could not be brought into flower under actual or simulated summer conditions. In these cultures, the daily photoperiod was extended by incandescent lights, when necessary, to between 16 and 20 hours. Later cultures were brought into flower, however, by simulating the fall conditions of the natural environment to the extent of materially reducing

¹ Supported by grant G-3886, National Science Foundation.

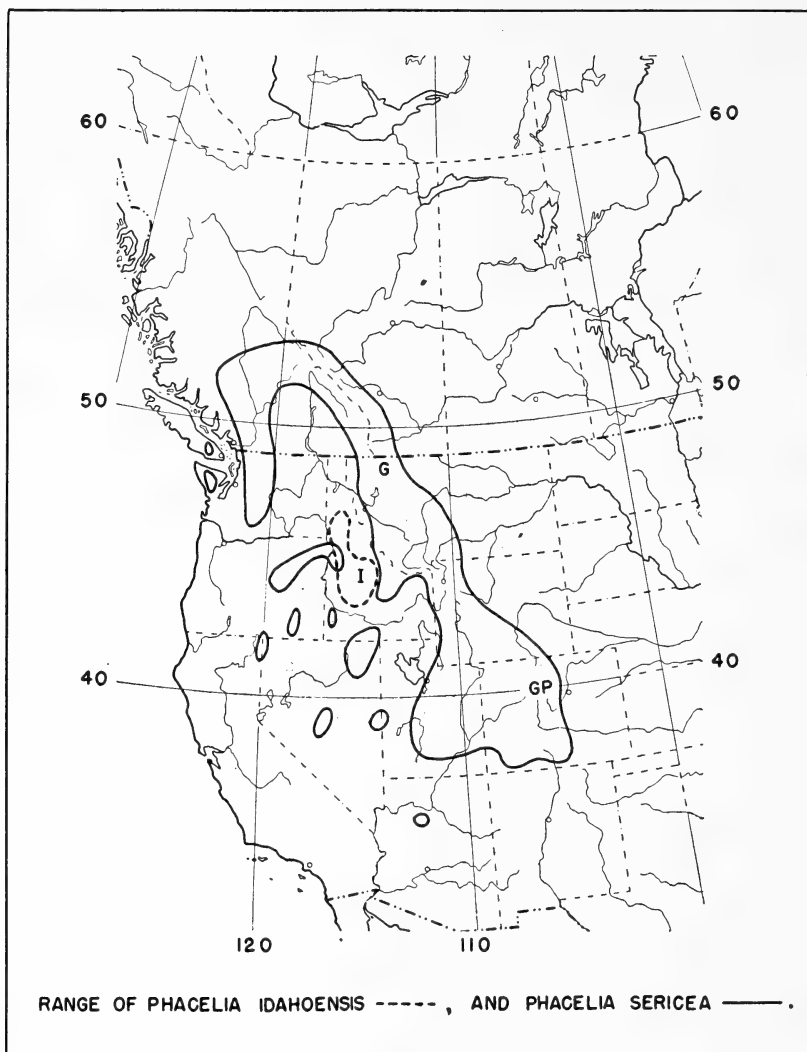


FIG. 1. Geographical distribution of *Phacelia sericea* and *Phacelia idahoensis*. Races employed in experimental cultures: *P. idahoensis* (I), Valley Co., Idaho. *P. sericea* subsp. *sericea*: (G), Glacier Co., Montana; (GP), Routt Co., Colorado. Base map courtesy of University of Chicago Press.

the length of the photoperiod and, at the same time, providing a cool temperature regime (Table 1). The data obtained from these cultures could be of value to those interested in growing alpine perennials experimentally, inasmuch as they show that certain alpine perennials can be manipulated into flowering in a relatively short time.

Both *Phacelia sericea* and *P. idahoensis* are spring-flowering perennials.

Early growth in each species is marked by the formation of a leaf rosette at ground level, with a virgate inflorescence axis later arising from the center of the rosette. In respect to geographical distribution (fig. 1), *P. sericea* occurs in the Rocky Mountains, the northern Cascades, the Olympics, and the ranges of the northern Great Basin. It is common at higher elevations, occurring on exposed gravel banks and talus slopes from 4500 feet, in the Canadian Rockies, to 13,000 feet in southern Colorado. By contrast, *P. idahoensis* is restricted to central Idaho, where it is found between 2800 and 7000 feet on wet meadows, stream banks, and on bottomlands subject to seasonal flooding.

Limited field studies made on colonies of *Phacelia sericea* subsp. *sericea* have produced some information about the flowering response in this cordilleran subspecies. In several colonies examined in Colorado, Wyoming, and Montana, there was a pronounced tendency for early summer flowering, and for the simultaneous expression of a given phase of flowering by both large and small plants within a given colony. Furthermore, widely-separated colonies that were examined on the same day exhibited similar stages of inflorescence development. These points were convincingly emphasized by an extensive and unsuccessful search for meiotic flower buds in several flowering colonies in Glacier County, Montana. In this area, and in Park County, Wyoming, colonies separated by as much as 1000 feet of elevation were found in similar stages of flowering.

The examination of collection data from over 800 herbarium sheets of *Phacelia sericea* and *P. idahoensis* confirmed the above field observations. In both species, there is a very strong tendency to early summer flowering, and general uniformity in the stage of inflorescence development in specimens of a given collection. The sum total of this evidence would, therefore, suggest that flowering in these species is "triggered" by a broadly imposed environmental stimulus or stimuli, and it would tend to rule out the possibility that these are day-neutral species.

Three races of these species were included in the present study. They were grown in experimental cultures (see Table 1) from seed collected in the following localities:

Phacelia sericea subsp. *sericea*

Gore Pass. Newly-graded road shoulder, highway 84, Routt County, Colorado, 9.9 miles west of Gore Pass, elevation ca. 8000 feet, Gillett 1145 ("GP" in fig. 1).

Glacier. Gravel road shoulder, 0.8 miles west of Many Glacier Entrance Station, Glacier National Park, Glacier County, Montana, elevation 4800 feet, Harry Robinson s.n. ("G" in fig. 1).

Phacelia idahoensis

Moist bottomlands 2.9 miles south of Donnelly, Valley County, Idaho, elevation 4800 feet, James Hockaday s.n. ("I" in fig. 1).

Voucher specimens of experimental plants have been deposited at the herbaria of Michigan State University and the University of California, Berkeley.

TABLE 1. FLOWERING RESPONSES IN PHACELIA IDAHOENSIS AND P. SERICEA

I. Plants given <i>long-day cycles only</i> .			
A. Approximately 155 long-day cycles between October and March, 18–20 hour photoperiods. Temperatures between 10° and 25°C.			
	<i>No. Plants</i>	<i>Flowered</i>	
<i>P. idahoensis</i>	9	0	
<i>P. sericea</i> (Gore Pass)	8	0	
<i>P. sericea</i> (Glacier)	5	0	
B. Approximately 180 long-day cycles between April and September; with 14–16-hour photoperiods. Temperatures between 15° and 30°C.			
<i>P. idahoensis</i>	20	0	
<i>P. sericea</i> (Gore Pass)	10	0	
<i>P. sericea</i> (Glacier)	10	0	
C. Approximately 250 long-day cycles between February and October; with 14–16-hour photoperiods. Temperature between —3° and 35°C.			
<i>P. idahoensis</i>	8	0	
<i>P. sericea</i> (Glacier)	4	0	
II. Plants given <i>long-day cycles (14–16 hr. photoperiods) followed by short-day cycles</i> . ^a			
A. Approximately 110 long-day cycles (temp. regime of I.-C) followed by 23 short-day ^b cycles terminated by 22 cycles of 16-hour photoperiods under 14°C. days and 7°C. nights, the 155-days-old plants then placed in a greenhouse (mid-July), with no supplementary light.			
	<i>No. Plants</i>	<i>Flowered</i>	<i>Days to flowering after short-day treatment</i>
<i>P. idahoensis</i>	8	8	16
<i>P. sericea</i> (Glacier)	4	2	12
B. Approximately 163 long-day cycles (temp. regime of I.-C) followed by 65 short-day ^c cycles, the 228-days-old plants then placed in a greenhouse (mid-September), with no supplementary light.			
<i>P. idahoensis</i>	3	3	19
<i>P. sericea</i> (Glacier)	2	1	16
C. Approximately 169 long-day cycles (temp. regime I.-C) followed by 59 short-day ^c cycles, the 228-days-old plants then placed in a greenhouse (mid-September), with no supplementary light.			
<i>P. idahoensis</i>	3	3	23
<i>P. sericea</i> (Glacier)	2	1	23
^a short-day cycles given inside a walk-in refrigerator with incandescent lights under temperature regime of 14°C. days and 7°C. nights.			
^b 10-hour photoperiods.			
^c 8-hour photoperiods.			

Culture techniques included germinating seeds in moist vermiculite, then transplanting young (ca. two weeks old) seedlings to four-inch pots holding equal parts of sterilized, screened river sand and peat moss. The plants were fed a nutrient solution (2 oz. commercial fertilizer per gallon of tap water) once a week through a siphon connection to the watering hose.

The light and temperature regimes provided for these cultures are given in Table 1. The results obtained indicate that *Phacelia sericea* subsp. *sericea* and *P. idahoensis* are neither day neutral nor "nominal" long-day plants. The positive flowering responses obtained in all cultures given the combination of cool temperatures and short photoperiods would suggest that these are obligate short-day species; although the possibility of their being conditioned for flowering by low temperatures, independent of day length, remains very strong.

In a final experiment, seven plants of *Phacelia idahoensis* that had been held to long photoperiods of from 14 to 16 hours for 264 days were placed in an open cold frame and exposed to the late fall light and temperature regime of central Michigan. These conditions included temperatures ranging from +10° to -10°C. After 37 days of "outside" weather, these plants, the pots frozen solid, were removed to the greenhouse. Six of the seven plants produced inflorescences and flowered within a month. These inflorescences were formed in a greenhouse where unaltered December lighting conditions prevailed, demonstrating (as indicated in II-C of Table 1) that this species does not require, subsequent to induction, a long-day regime for flowering. It would seem practicable, therefore, to culture this species by a schedule that would include spring germination, and a fall induction period under a cool temperature regime, with the prevailing light of approximately 40° north latitude. It is probable that these suggestions also apply to *P. sericea* subsp. *sericea* inasmuch as its flowering response is similar. A close relationship is indicated by the genetic compatibility between the two taxa, the F₁ hybrids being highly fertile and also flowering after short-day induction treatments.

In addition to providing knowledge for the successful culture of these and probably other species of alpine perennials, these experiments leave a pointed suggestion for plant geographers, namely, that *Phacelia sericea* subsp. *sericea*, a northern alpine perennial, has, in terms of photoperiod requirements, southerly rather than arctic affinities. This would not be surprising in view of the fact that the great bulk of *Phacelia* species are found south of 40° north latitude, while only two species occur farther north than *P. sericea* subsp. *sericea*.

Department of Botany and Plant Pathology
Michigan State University, East Lansing

REVIEWS

Illustrated Flora of the Pacific States. Washington, Oregon, and California. Volume IV—Bignoniaceae to Compositae. By ROXANA STINCHFIELD FERRIS. xiii + 732 pages, 1124 figures, and an appendix (for all four volumes) with key to families, index to common names, and index to scientific names. Stanford University Press, Stanford, California. 1960. \$17.50.

In 1923, with the publication of Volume I, Ophioglossaceae to Aristolochiaceae, of the "Illustrated Flora of the Pacific States," Leroy Abrams launched his life's work—an illustrated, descriptive flora of all vascular plants known to grow wild in the three Pacific states—Washington, Oregon, and California. Now, thirty-seven

years later, with the publication on January 22, 1960, of Volume IV, Bignoniaceae to Compositae, by Roxana Stinchfield Ferris, the monumentally conceived project is completed and a milestone in the floristic botany of the western states is achieved. Although the task outlasted the life-time and efforts of Professor Abrams, who died in 1956 after about eight years of failing health, he was very fortunate in having the collaboration and devoted assistance of Mrs. Ferris almost from the beginning of the project, and progress on the flora continued uninterruptedly through the years. Mrs. Ferris gave increasing effort to Volume II, Polygonaceae to Krameriaceae, published in 1944, and the task fell upon her of finishing Volume III, Geraniaceae to Scrophulariaceae, published in 1951. She had the entire responsibility for Volume IV. That the finished work ably carries out the objectives stated in Volume I—"to furnish an authentic reference book that will be of greatest service not only to the trained botanist but to everyone interested in the native plant life of the Pacific States."—is tribute not only to Professor Abrams' vision and high level of scholarship but also to Mrs. Ferris' devoted and able efforts toward full realization of his goals.

The "Illustrated Flora of the Pacific States" was designed to duplicate for western botany what Britton and Brown, in their "An Illustrated Flora of the Northern United States, Canada and the British Possessions," had done for eastern botany. These are the only two great North American floristic works in which all species are illustrated and in which the illustrations share along with keys and descriptions the task of species identification. Abrams not only followed the general pattern set by Britton and Brown, but, at first, also followed them in their use of the "American Code" for nomenclature. With the adoption of the International Code after the international congresses of 1930 and 1935, however, the two "codes" were brought almost into accord, and in the 1940 reprinting of Volume I of his flora, Abrams made such generic changes as were necessary to bring his nomenclature into conformity with the International Rules.

In all four volumes specialists were invited to contribute the text for certain plant groups, and in Volume IV Mrs. Ferris had the able assistance of ten such collaborators. In addition she was fortunate in being able to base her treatment of the Compositae as a whole upon extensive manuscript notes from the late Dr. Sidney Fay Blake, who had originally planned to contribute the entire text for this family. Mrs. Ferris wrote the major part of the volume herself, however, and, in many groups such as *Baeria*, *Plantago*, and *Galium*, to name a few, she made significant contributions toward clarification of our understanding of the species.

The illustrations deserve especial consideration inasmuch as they are an integral part of the plan of the entire work. In Volume IV, following the general plan of preceding volumes, the illustration for each species consists of a group of carefully arranged line drawings occupying a rectangle about 2 x 3 inches. There may be two or three or as many as eight separate drawings artistically combined within the given rectangle in such a way as to give both overall aspect or habit of the plant and significant structural details, a combination necessitating much ingenuity and skill. These illustrations of species are then grouped six to a page, or in some cases two or four illustrations may occupy a third or two-thirds of a page. It is stated in the preface that the illustrations, except for the structural features, are half size unless otherwise marked. Legends are confined to binomials, but the pertinent information in the carefully worded text is close at hand, the illustrations and descriptions thus complementing each other and obviating the need for detailed legends. Most of the drawings in Volume IV were made by Jeanne Russell Janish, who was also the artist for many of the illustrations in volumes II and III. Many of the drawings of the Compositae in Volume IV, however, were made by Doris Holm Blake while her husband, Sidney Fay Blake, was working upon what he then hoped would culminate in his full text for the Compositae. The drawings for *Agoseris* and *Helianthus* were made by other artists under supervision of the specialists who contributed the texts for these genera. Except for a few cases where detail is obscured by the illustrations being overly black, reproduction is excellent.

Throughout the volume the keys are skillfully and evenly handled despite the number of different contributors. There are some unfortunate instances of the use of a negative rather than a truly opposing phrase in the second branch of a key dichotomy, but understandably these instances occur particularly in the "difficult" groups. One of the major tasks in preparation of Volume IV was the assembling of an appendix for all four volumes. This contains 1) a key to the families, 2) an index of common names, and 3) an index to scientific names. The family key gives not only the family numbers but also the volume and page on which each family is found, a very necessary aid in a work of this magnitude. The index to common names (there is a common name for every species treated in the four volumes) has the family names printed in small capitals and the genera in Roman type. The index to scientific names is much longer and more complicated than that to common names, having approximately 17,500 entries occupying 79 pages. It has the names of families and tribes printed in small capitals, the genera, species, subspecies, and varieties in Roman type, and the synonyms in italics, all appropriately indented. Because some groups have a great number of species as well as many generic and specific synonyms, the genera in the index to scientific names are not always easy to locate. Possibly greater indentation or perhaps the use of boldface type for generic names would have made them stand out more, although to do this would have necessitated a departure from the style of the previous volumes.

The Stanford University Press has achieved another outstanding accomplishment in typography, printing, and binding, and the volume contains a minimum of typographical and other mechanical errors.

Dr. Bacigalupi, curator of the Jepson Herbarium, has given me permission to quote from the unpublished field notebook of Willis Linn Jepson, whose entry for February 3, 1910, reads: "I am just receiving the first reviews of my *Flora of California*, Pts. 1 and 2. The critics mostly or even entirely confine themselves to verbal slips, not touching general principles. It is, to be sure, disconcerting enough to have such errors, but after all the main thing is this: 'Has the book got matter in it? Has it got stuff in it? Is it meaty? Not is it *faultless*. A faultless book is impossible. It is inevitable in the nature of the human mind that such slips will be made, mistakes and blunders. But is the job a big one, is it really worthwhile? So satisfied am I in the affirmative that it is a big task, to be done in a big way, without too much considering the danger of possible minor errors, that I go on, to finish up my job, just as other big jobs have been finished aforetime.'"

All will agree that Mrs. Ferris' job has got matter, stuff, and meat in it, that it was a big task, done in a big way.—HELEN K. SHARSMITH, Department of Botany, University of California, Berkeley.

Experimental Studies on the Nature of Species. IV. Genetic Structure of Ecological Races. By JENS CLAUSEN and W. M. HIESEY. Carnegie Institution of Washington Publication 615. Washington, D.C. Octavo, vii + 312 pp., 33 figs. 1958. Paper \$4.25, cloth \$4.75.

This is the fourth in the series of scholarly monographs based on the studies of plant evolution conducted by these authors over the past three decades. This newest volume expands the earlier work on the evolutionary importance of ecological races by considering in detail the genetics of the altitudinal races of *Potentilla glandulosa* and then reviewing examples from the literature on the genetic structure of ecological races.

The volume is organized into five chapters and although these are skillfully inter-related they are sufficiently distinct and different to require individual comment. Chapter I, *Ecological Races of P. glandulosa*, introduces the general topic of the volume by presenting what might be called the systematics of *P. glandulosa* as it occurs along the altitudinal transect across central California. This adroitly prepared chapter makes it possible to read the work without reviewing the previous publications by these authors on *P. glandulosa*. Chapter II, *Genetics of Ecological Races*,

comprises nearly one third of the entire work. The first portion describes the crosses made between selected plants of the various climatic races of *P. glandulosa* by giving in detail the characteristics of the parental plants and the segregation of these characteristics in the F_1 , F_2 and F_3 generations. Of particular interest here is the use of punched cards for recording and analyzing the data on 14 different characteristics of each individual plant in these crosses. The inherent nature of the punched card system gave an index number series for each character and a summation of these gave an index value for each plant that proved useful in the general comparison of parents and their progenies. Frequency distribution of parent index values and hybrid index values are presented and give a picture of the spectrum seen in the segregation of the F_2 from the crosses between the contrasting ecological races. The second section of Chapter II presents analyses of the segregation ratios by proposing gene systems that could account for the complex ratios observed. These analyses are detailed to the point of proposing for each characteristic the number of loci involved, the number of alleles at each locus, and the action and interactions of the various genes. The significance of these proposed gene systems lies not in their accuracy as to details but rather lies in the fact that viewed collectively they demonstrate that the differences between the ecological races are controlled by units of segregation and recombination that can be described in terms of classical genetics. These points are clearly expressed in the concluding chapter.

Chapter III, *Response Patterns at Contrasting Altitudes*, analyzes the responses of cloned individuals of an F_2 between two ecological races to the different environments of the transplant stations. Studying such an F_2 under different natural environments leads the authors to estimate the evolutionary potential of segregating populations. They conclude this important chapter with the following: "The present races are the products of long-time selection, and have attained an equilibrium with their environments. Natural selection will therefore tend to favor the original racial combination as long as the over-all genetic structure and the habitats remain the same, although a certain amount of introgression may take place. Over long periods genes may gradually migrate across long distances from the original point of contact and may finally appear in combination where they have selective value."

Chapter IV, *Systems of Genes Controlling Characters and their Significance in Environmental Adaptation and Evolution*, is the longest chapter comprising over one third of the text material. It differs markedly from the previous three chapters in that it does not present new data but rather reviews a considerable segment of the genetic literature dealing with gene systems. The relevance of these reviews to the previous chapters lies in the fact that the gene systems discussed are of the same general sort as the gene system for *P. glandulosa*. Chapter V, *Concepts of the Genetic Structure of Ecological Races*, develops a general concept of the genetic structure and evolutionary importance of ecological races.

In the tradition of the previous volumes a vast amount of the original data are presented in a tabular form and the same precise, clear writing and excellent illustration are evident.

The strength of this book clearly lies in the work on *P. glandulosa*. Hybridization studies and the observation of the responses of cloned individuals to different natural environments are two of the powerful tools of evolutionists. In combining both of these approaches in the study of *P. glandulosa* the authors present a new dimension of information about natural populations. At this moment we cannot predict the amount of influence this publication will have on our understanding of evolution. We can be sure, however, that it will remain the classic work of its kind for many years because the time, facilities, and skills necessary for this type of study are available to few botanists.—HENRY J. THOMPSON, Department of Botany, University of California, Los Angeles.

INDEX TO VOLUME XV

Classified entries: Chromosome numbers, Reviews. New scientific names are in boldface type. Un-annotated taxa in floral lists are omitted from Index.

- Acer circinatum*, 227
Alliaria officinalis, 96
Allium: *macrum*, 226; *nevii*, 226; *tolmiei*, 227
Angelica: *canbyi*, 227; *genuflexa*, 230
Anthriscus scandicina, 229
Arceuthobium: *americanum*, 130; *cam-pylopodum*, 132; *douglasii*, 137; dwarf mistletoes, in California, 129
 Arnott, H. J., *Vivipary in Cordyline australis* Hook., 71
Aster: New combinations in, 128; *occidentalis* var. **delectabilis**, 128, var. **parishii**, 128
Atriplex confertifolia, 227
 Bacigalupi, R.: G. Thomas Robbins, 231
 Baker, M. S., *Studies in western violets*, IX, Sections *Nomimium* and *Chamaemelanium*, 199
Beckmannia syzigachne, 64
 Benson, L., *Typification of Prosopis odorata* Torr. & Frem. 53
Bupleurum rotundifolium, 64
Campanula scouleri, 228
Cardamine oligosperma, 229
Cardiocrinon late-alatum, 180, fig. 182
Cardiospermum halicacabum, 64
Carex: *aperta*, 229; *eurycarpa*, 226
 Carter, A., *Urospermum picroides* (L.) Schmidt in Berkeley, 224
Ceanothus cordulatus, 80; *integerrimus*, 80; seeds and seedlings on burns, 79
Choreocolax: *margaritoides*, 33; *polysiphoniae*, 33; *suhriae*, 33
 Chromosome numbers: *Agastache urticifolia*, 51; *Amsonia brevifolia*, 50, var. *tomentosa*, 50; *Astragalus bolanderi*, 82, *crotalariae*, 82, *leucopsis*, 82, *oocarpus*, 82, *pomonensis*, 82; *Blennosperma nanum* var. *robustum*, 220; *Cathartolinum digynum*, 49; *Chaenactis douglasii*, 52; *Chamaesaracha nana*, 51; *Chrysopsis foliosa*, 52; *Coldenia canescens*, 50, *palmeri*, 50, *plicata*, 50, *purpusii*, 50; *Cryptantha pterocarya*, 50; *Datisca glomerata*, 82; *Datura meteloides*, 83; *Delphinium carolinianum*, 219, *polycladon*, 82, *virescens* var. *macroceratilis*, 219; *Dithyrea californica*, 49; *Encelia frutescens*, 220; *Epilobium obcordatum*, 82; *Erysimum capitatum* var. *bealianum*, 49; *Eschscholtzia mexicana*, 82; *Fraxinus velutina*, 161, var. *coriacea*, 161; *Fritillaria biflora*, 82; *Garrya lindheimeri*, 220; *Gayophytum helleri* var. *glabrum*, 91, *humile*, 91, *lasiospermum*, 91, *nuttallii*, 91, var. *abramsii*, 91, *racemosum*, 82, var. *erosulatum*, 91, *ramosissimum*, 92; *Glandularia canadensis*, 51, *gooddingii*, 50, *perackii*, 50; *Haplopappus ciliatus*, 52, *divaricatus*, 52, *hartwegii*, 52, *havardii*, 220, *phyllocephalus* subsp. *annuus*, 220, subsp. *phyllocephalus*, 220, *pleuriflorus*, 52, *spinulosus*, 220; *Helianthus ciliaris*, 57, *crenatus*, 57; *Heliotropium parviflorum*, 50; *Hesperocallis undulata*, 49; *Isomeris arborea*, 82; *Lupinus superbus* var. *elongatus*, 82; *Lychnis drummondii*, 205, *wilfordii*, 206; *Lyrocarpa palmeri*, 49; *Machaeranthera blephariphylla*, 221, *gymnocephala*, 52, *tagetina*, 221, *tanacetifolia*, 52; *Marah macrocarpus*, 52; *Mimulus glabratus* var. *fremontii*, 243, var. *parviflorus*, 59, var. *utahensis*, 243, *glaucescens*, 59, *guttatus*, 59, 242, *lacinatus*, 242, *laxus*, 242, *luteus*, 61, 243, *nasutus*, 242, *pilosiusculus*, 59, *platycalyx*, 243, *tigrinus*, 59, 243, *tilingii* var. *corallinus*, 59, var. *tilingii*, 59, 242; *Monardella cinerea*, 51, *lanceolata*, 51, *linoides*, 51, *odoratissima*, 82; *Myosotis versicolor*, 50, *aristatus* subsp. *montanus*, 140, *cupulatus*, 140, *minimus*, 139, var. *filiformis*, 140, subsp. *apus*, 140, *sessilis*, 140, subsp. *alopecurioides*, 140; *Neptunia dimorphantha*, 185, *gracilis*, 185, *lutea*, 185, *monosperma*, 185, *plena*, 185, *prostrata*, 185, *pubescens* var. *floridana*, 185, var. *lindheimeri*, 185, *triquetra*, 185; *Nolina parryi*, 49; *Oenothera californica*, 82; *Orthocarpus attenuatus*, 51, *linearilobus*, 51, *purpurascens*, 51; *Pedicularis groenlandica*, 83; *Penstemon clutei*, 220; *Petrocoptis pyrenaica*, 206, 215; *Plantago insularis*, 83; *Porophyllum scoparium*, 221; *Proboscidea jussieu*, 83; *Pseudotaenidia montana*, 220; *Psilostrophe cooperi*, 221; *Ranunculus californicus*, 82, *occidentalis* var. *eisenii*, 49; *Ratibida columnaris*, 52, *peduncularis* var. *picta*, 52, *tagetes*, 52; *Saxifraga ferruginea*, 219, *integri-folia*, 219, *montanensis*, 219, *occidentalis*, 219, *tolmiei*, 220; *Sclerocarpus uniserialis*, 221; *Senecio fremontii* var. *occidentalis*, 83, *longilobus*, 52; *Silene antirrhina*, 206, *aperta*, 205, *bridgesii*, 173, 205, *californica*, 205, *campanulata*, 173, 205, *caroliniana*, 206, subsp. *wherryi*, 206, *clokeyi*, 205, *douglasii*,

- 205, grayi, 205, hookeri, 205, invis, 205, keiskei, 206, laciniata subsp. greggii, 205, subsp. major, 205, lemmonii, 173, 205, marmorensis, 173, 176, 206, menziesii, 206, montana, 206, nuda, 206, subsp. insectivora, 206, occidentalis, 206, oregana, 206, parishii, 206, parryi, 206, petersonii, 206 polypetala, 206, regia, 206 repens subsp. australis, 206, var. latifolia, 206, rotundifolia, 206, sargentii, 206, scaposa, 206, scouleri, 206, spaldingii, 206, stellata, 206, struthioloides, 206, subciliata, 206, thurberi, 206, verecunda subsp. andersonii, 206, subsp. platyota, 206, subsp. verecunda, 206, virginica, 206, williamsii, 206, wrightii, 206; Solanum xantii, 51; Streptanthus inflatus, 49; Thelypodium lasiophyllum, 82; Verbena bracteata, 51, 220, hastata, 220, prostrata, 51, stricta, 220, urticifolia, 220; Viguiera adenophylla, 221, deltoidea var. parishii, 221, dentata var. brevipes, 221, porteri, 221, stenoloba, 221; Viola bakeri subsp. bakeri, 204, subsp. shastensis, 204, praemorsa subsp. arida, 204, subsp. oregona, 204; Zigadenus brevibracteatus, 49; Zinnia acerosa, 216, citrea, 216, grandiflora, 52, 216
- Chromosome numbers of plants, Documented, 49, 82, 219
- Clarkson, Q. D., Field studies of natural hybridization in the Oregon species of Iris L. subsec. Californicae Diels, 115
- Copeland, H. F.: The reproductive structures of Fraxinus velutina (Oleaceae), 161; The reproductive structures of Schinus molle (Anacardiaceae), 14
- Cordylina: australis, 71; Vivipary in, 71
- Crampton, B., The grass genera Orcuttia and Neostaphia; a study in habitat and morphological specialization, 97
- Cucurbita: interspecific cross in, 4; lundelliana, 4, fig. 6, fig. 8, fig. 10; moschata, 4, fig. 6, fig. 8, fig. 10
- Cupressus: abramsiana, 1; goveniana, 1; macrocarpa, 3; pygmaea, 1; sargentii, 1; in pygmy forests of Mendocino County, 1
- Dasystephana newberryi, 234
- Datura meteloides, 87, fig. 85
- Davidson, J. F., Cleared Cardiocarpon late-alatum Lesq. Cordaitean seeds from Michigan, 180
- Dixon, D. G., Chromosome counts in the genus Gayophytum, 90
- Echinodorus berteroi, 64
- Fan, K.-C., and G. F. Papenfuss, Red algal parasites occurring on members of the Gelidiales, 33
- Fearing, O. S., and B. L. Turner, The basic chromosome number of the genus Neptunia, 184
- Ferris, R. S., New combinations in Aster, 128
- Flint, F. F., Development of the magagametophyte in Liquidambar styraciflua L., 25
- Fraxinus velutina, 161, fig. 163, fig. 165, fig. 167; The reproductive structures of, 161
- French, D. H., and R. Ornduff, Distributional notes on plants of the Warm Springs area, Oregon, 225
- Fritillaria biflora, 83, fig. 85
- Gayophytum: Chromosome counts in, 90; helleri var. glabrum, 92
- Gelidiales, Red algal parasites of, 33
- Gelidiocolax: **mammillata**, 34, figs. 35-37; **margaritoides**, 34; microsphaerica, 33; **suhriae**, 33
- Gentiana: copelandii, 234; eximia, 234; newberryi, 234; newberryi and G. tiogana, Studies in the perennial gentians, 233; tiogana, 235
- Gillett, G. W.: Flowering responses in Phacelia sericea and P. idahoensis, 245
- Gray, J., Review, Pollen and spore morphology/plant taxonomy, 62
- Greene, Edward Lee, Correspondence, 222
- Haller, J. R., Factors affecting the distribution of Ponderosa and Jeffrey pines in California, 65
- Helianthus: ciliaris, 54; **crenatus**, 55; **heiseri**, 54; Two new species of, from New Mexico, 54
- Hoffman, Freed, 178
- Iris: bracteata, 120; bracteata \times chrysophylla, 121; chrysophylla, 116; douglasiana, 119; douglasiana \times innominata, 120; innominata, 119; Field studies of natural hybridization in the Oregon species of, subsection Californicae Diels, 115; tenax, 116, subsp. bracteata, 121, subsp. chrysophylla, 121, subsp. douglasiana, 122, subsp. innominata, 122, subsp. tenax, 121, subsp. thompsonii, 122; subsection Californicae, hybridization in, 115; thompsonii, 120
- Isomeris arborea, 84, fig. 85
- Jackson, R. C., Two new species of Helianthus from New Mexico, 54
- Jeffrey and Ponderosa pines: A comment on cold susceptibility of, 217; Distribution of, in California, 65
- Kasapliligil, B., Review, Die Nadelgehölze, 30

- Kruckeberg, A. R.: A new *Silene* from northwestern California, 172; Chromosome numbers in *Silene* (Caryophyllaceae), II, 205
- Kuijt, J.: Occurrence of *Pilostyles thurberi* in California, 63; The distribution of dwarf mistletoes, *Arceuthobium*, in California, 129
- Liquidambar styraciflua*, 25, figs. 26–27; megagametophyte development, 25
- Lomatium*: *cous*, 227; *leptocarpum*, 227; *nevadense*, 228
- Lupinus superbus* var. *elongatus*, 86
- Lychnis wilfordii*, fig. 211
- Major, J., Review, *Carex*, its distribution and importance in Utah, 221
- Mason, C. T., Jr.: Notes on the flora of Arizona, 64; Studies in the perennial gentians, *G. newberryi* and *tiogana*, 233
- Mathias, M. E., and Raven, P. H., *Sanicula deserticola*, an endemic of Baja California, 193
- Maule, S. M., *Xerophyllum tenax*, squawgrass on Mount Rainier, 39
- McIntosh, R. P., Edward Lee Greene correspondence, 222
- McMillan, C., Survival of transplanted *Cupressus* in the pygmy forests of Mendocino County, California, 1
- McVaugh, R., Review, Spring flora of the Dallas-Fort Worth area, 94
- Mertensia*: *ciliata*, 123, Variation patterns in, 123; *fusiformis*, 123
- Meyer, F. G., A new species of *Valeriana* from Brazil, 197
- Mimulus*: Chromosome counts in section *Simiolus* of, 57, 239; *glabratus* var. *fremontii*, 243, var. *parviflorus*, 58, var. *utahensis*, 243; *glaucescens*, 58; *guttatus*, 58, 242; *laciniatus*, 242; *laxus*, 242; *luteus*, 61, 243; *nasutus*, 242; *pilosusculus*, 58; *platycalyx*, 243; *tigrinus*, 58, 243; *tilingii*, 242, var. *corallinus*, 58, var. *tilingii*, 58
- Mirov, N. T., Review, The physiology of forest trees, 192
- Morrison, J. L., Freed Hoffman, 178
- Mukherjee, B. B., and R. K. Vickery, Jr.: Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae), III, 57; IV, 239
- Myosotis micrantha*, 229
- Myosurus*: *aristatus*, fig. 146; *cupulatus*, fig. 141, fig. 146; *minimus*, fig. 144, subsp. *apus*, fig. 144, var. *filiformis*, fig. 141, fig. 145; Nuclear cytology, 139; sessilis, figs. 141–142
- Neosecotium*: 154; *africanum*, 156; *macrosporum*, 154, fig. 155; and *Secotium*, 152
- Neostapfia*: 97; and *Orcuttia*, 97
- Neptunia*, The basic chromosome number of the genus, 184
- Nicotiana*: *palmeri*, 148; *trigonophylla*, 148; Variation in section *Trigonophyllae*, 148
- Notes and News, 32, 63, 96, 128, 160, 192, 222
- Oenothera californica* var. *californica*, 87
- Orcuttia*: and *Neostapfia*, habitat and morphological specialization, 97; *californica* var. *inaequalis*, 99, var. *viscida*, 103; *greenei*, 102; *mucronata*, 107, figs. 106–107; *pilosa*, 99; *tenuis*, 103
- Ornduff, R.: *Alliaria officinalis* in Oregon, 96; Review, Spring flowers of lower Columbia Valley, 94; and D. H. French, Distributional notes on plants of the Warm Springs area, Oregon, 225
- Panicum pacificum*, 226
- Papenfuss, G. F., and Fan, K.-C., Red algal parasites occurring on members of the *Gelidiales*, 33
- Pelton, J. S., Variation patterns in four clones of *Mertensia ciliata*, 123
- Phacelia*: *idahoensis*, 247; *sericea*, 247; *sericea* and *idahoensis*, Flowering responses in, 245
- Picea*: *engelmannii*, 111, and *P. glauca*, The taxonomic relationship between, 111; *glauca*, 111, subsp. *engelmannii*, 114, subsp. *glauca*, 114
- Pilostyles thurberi* in California, 63
- Pinus*: *jeffreyi*, 65, 217; *ponderosa*, 65, 217
- Pneumonanthe newberryi*, 234
- Ponderosa* and *Jeffrey* pines: cold susceptibility of, 217; Distribution of, in California, 65
- Prosopis*: *glandulosa*, 53; *juliflora* var. *glandulosa*, 53, var. *torreyana*, 53, var. *velutina*, 53; *odorata*, 53, Typification of, 53; *pubescens*, 53
- Pterocladophyllaceae**, 38
- Pterocladophila hemisphaerica*, 34, figs. 35–36
- Pteryxia terebinthina*, 228
- Quick, C. R., *Ceanothus* seeds and seedlings on burns, 79
- Raven, P. H., and Mathias, M. E., *Sanicula deserticola*, an endemic of Baja California, 193
- Reviews: Clausen, J., and W. M. Hiesey, Experimental studies on the nature of species, IV, Genetic structure of ecological races, 251; Erdtman, Pollen and spore morphology/plant taxonomy, 62; Ferris, R. S., Illustrated flora

- of the Pacific States—Washington, Oregon, and California, Volume IV, Bignoniaceae to Compositae, 249; Foster, A. S., and Gifford, E. M., Jr., Comparative morphology of vascular plants, 158; Hill, Spring flowers of the lower Columbia Valley, 94; Howell, J. T., P. H. Raven, and P. Rubtsoff, A flora of San Francisco, 29; Krüssmann, G., Die Nadelgehölze, 30; Lewis, M. E. *Carex*, its distribution and importance in Utah, 221; Shimmers, Spring flora of the Dallas-Fort Worth area, 94; Thimann, K. V., et al., editors, The physiology of forest trees, 192
- Robbins, G. Thomas, 231
- Rubus laciniatus*, 228
- Salix drummondiana* var. *subcoerulea*, 227
- Sanicula*: *bipinnatifida*, 194; *deserticola*, 193, endemic of Baja California, 193
- Schinus molle*, 14, fig. 15, fig. 17, fig. 20, The reproductive structures of, 14
- Secotium*: *aurantium*, 73; *gueinzii*, 152, table 157; *macrosporum*, 153; and *Neosecotium*, Studies on secotiaceous fungi VII, 152; *tenuipes*, 73
- Senecio*: *fremontii* var. *occidentalis*, 88, fig. 85; *macounii*, 228
- Setchelliiogaster*: 74; *aurantium*, 76; *tenuipes*, 74, fig. 77
- Sharsmith, H. K.: Review, Illustrated flora of Pacific States, Vol. IV, 249
- Silene*: *antirrhina*, fig. 211; *aperta*, fig. 209; *bridgesii*, 173; *californica*, 207; *campanulata*, 173, 210; *caroliniana*, fig. 211, subsp. *wherryi*, fig. 211; Chromosome numbers in, 205; *clokeyi*, fig. 209; *douglasii*, 210; *grayi*, fig. 209; *hookeri*, 207; *invisa*, fig. 209; *keiskei*, fig. 211; *laciniata* subsp. *laciniata*, 207, subsp. *greggii*, 207, fig. 209, subsp. *major*, 207; *lemmonii*, 173, fig. 209; *marmorensis*, 174, figs. 175—177; *menziesii*, 208; *montana*, fig. 209; New, from northwestern California, 172; *nuda*, 213, subsp. *insectivora*, 213; *occidentalis*, 213, fig. 209; *oregana*, 213; *parishii*, 213; *parryi*, 208; *petersonii*, fig. 209; *polypetalata*, fig. 211; *regia*, fig. 211; *repens* subsp. *australis*, fig. 209, var. *latifolia*, fig. 211; *rotundifolia*, fig. 211; *sargentii*, 213; *scaposa*, fig. 209; *scouleri*, 214; *seeleyi*, 210; *spaldingii*, fig. 209; *struthioloides*, fig. 211; *subciliata*, fig. 211; *thurberi*, fig. 211; *verecunda* subsp. *andersonii*, 214, subsp. *platyota*, 214, subsp. *verecunda*, 214, subsp. *virginica*, 215; *williamsii*, 210, fig. 211; *wrightii*, fig. 211
- Smith, A. H., and R. Singer: Studies on secotiaceous fungi VI, *Setchelliiogaster* Pouzar, 73; VII, *Secotium* and *Neosecotium*, 152
- Snow, R., Chromosome numbers of California plants, with notes on some cases of cytological interest, 81
- Stone, D. E., Nuclear cytology of California mouse-tails (*Myosurus*), 139
- Stylocline filaginea*, 228
- Syringocolax macroblepharis*, 33
- Taylor, T. M. C., The taxonomic relationship between *Picea glauca* (Moench) Voss and *Picea engelmannii* Parry, 111
- Tepfer, S., Review, Comparative morphology of vascular plants, 158
- Tetradymia glabrata*, 228
- Thomas, J. H., Review, A flora of San Francisco, 29
- Thompson, H. J., Review, Experimental studies on nature of species, IV, 251
- Torres, A. M., A new species of *Zinnia* from Mexico, 215
- Turner, B. L. and O. S. Fearing, The basic chromosome number of the genus *Neptunia* (Leguminosae — Mimosoideae), 184
- Urospermum picroides*, 224
- Valeriana*: A new species of, from Brazil, 197; *glechomifolia*, 197, fig. 198
- Vickery, R. K., Jr., and B. B. Mukherjee: Chromosome counts in the section *Simiolus* of the genus *Mimulus* (Scrophulariaceae), III, 57; IV, 239
- Viola*: *adunca*, 202; *aliceae*, 199, fig. 201; *bakeri*, 203, subsp. *shastensis*, 203; *lobata* subsp. *psychodes*, 200, fig. 201; *oxyceras*, 202, fig. 201; *praemorsa*, 204; *psychodes*, 200
- Wagner, W. W., A comment on cold susceptibility of *Ponderosa* and Jeffrey pines, 217
- Webber, J. M., Hybridization and instability of *Yucca*, 187
- Wells, P. V., Variation in section *Trigonophyllae* of *Nicotiana*, 148
- Whitaker, T. W., An interspecific cross in *Cucurbita* (*C. lundelliana* Bailey × *C. moschata* Duch.) 4
- Xerophyllum tenax* on Mount Rainier, 39
- Yucca*: *arizonica*, 188, fig. 189, × *glauca*, 190, fig. 189, × *neomexicana*, 190, fig. 189; *constricta*, 188, fig. 189, × *schidigera*, 188, fig. 189; *elata*, 188; *glauca*, 190, fig. 188, × *elata*, 188; Hybridization and instability of, 187; *neomexicana*, 188; *schidigera*, 188
- Zinnia*: A new species of, from Mexico, 215; *acerosa*, 216; *citrea*, 215; *grandiflora*, 216

INFORMATION FOR CONTRIBUTORS

Manuscripts submitted for publication should not exceed an estimated 20 pages when printed unless the author agree to bear the cost of the additional pages at the rate of \$20 per page. Illustrative materials (including "typographically difficult" matter) in excess of 30 per cent for papers up to 10 pages and 20 per cent for longer papers are chargeable to the author. Subject to the approval of the Editorial Board, manuscripts may be published ahead of schedule, as additional pages to an issue, provided the author assume the complete cost of publication.

Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

Articles may be submitted to any member of the Editorial Board.

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at the following rates:

Volume I, 1916-1929	\$5.00
Volume II, 1930-1934	5.00
Volume III, 1935-1936	5.00
Volume IV, 1937-1938	5.00
Volume V, 1939-1940	5.00
Volume VI, 1941-1942	5.00
Volume VII, 1943-1944	5.00
Volume VIII, 1945-1946	5.00
Volume IX, 1947-1948	6.00
Volume X, 1949-1950	7.00
Volume XI, 1951-1952	8.00
Volume XII, 1953-1954	8.00
Volume XIII, 1955-1956	8.00
Volume XIV, 1957-1958	8.00
Single numbers, Volumes 1 and 250
Succeeding numbers, (except Volume XI, No. 2)	1.00
Volume XI, No. 2	1.50

The subscription price of MADROÑO is \$6.00 per year. If your institution does not now subscribe to MADROÑO, we would be grateful if you would make the necessary request. Since there is no extra charge for institutional subscriptions, an individual may hold membership in the California Botanical Society on the basis of his institution's subscription.

Address all orders to:

FRANCIA CHISAKI, Corresponding Secretary
Department of Botany
University of California, Berkeley 4, California









SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01111 8080